

THE PROBABLE HISTORY OF SPECIES FORMATION IN SOME NORTHERN WOOD WARBLERS (PARULIDAE)

ROBERT M. MENGEL

Zoologists today are virtually agreed (Mayr, 1963:480, 513) that species formation in warm-blooded vertebrates is a process requiring geographical isolation of stocks ("allopatry") long enough for the development of morphological, physiological, or psychological isolating mechanisms adequate to insure continued genetic separation in case of renewed coexistence, or "sympatry."

How exquisitely complicated, then, must be the history of geographical isolations and distributional changes resulting in the many complex arrays of closely related genera and species of birds found in many parts of the world. But, while the classical examples in certain groups of oceanic islands have invited analysis—Darwin's finches in the Galápagos (Lack, 1947) and the Hawaiian honeycreepers (Amadon, 1950)—continental complexes conspicuously suggesting the history of the formation of numerous species from one or a few ancestral forms seem, at least, to be extremely rare.

This is because the antecedent events, especially due to the oft-lamented deficiencies in the avian fossil record, are usually shrouded in mystery, if not irretrievably lost to knowledge. Unlike the oceanic islands, the ecological "islands," presumably effective in multiplication of species on continents, have appeared, disappeared, and shifted, often leaving no evidence of their existence other than the multiplicity of species itself.

If there are exceptions, it seems logical to seek them among groups of species whose present distributions may be meaningfully interpreted in light of the considerable and rapidly-growing body of fact concerning the Pleistocene (or Ice Age), the most recent and hence best known geological epoch.

Although "the analysis of Pleistocene speciation has just begun" (Mayr, 1963:561), it must be admitted that early findings have been rather meager, especially in Europe, of which it has been said (whether or not too pessimistically) that "it cannot be shown with certainty that even a single glacial isolate . . . reached full species level" (Mayr, 1951; 1963:561). In North America, although a considerable number of pairs of (chiefly) eastern and western species shows clear evidence of resulting from Pleistocene separation of parental stocks (Rand, 1948), almost nothing has been suggested about the evolutionary history of more complex aggregations. It seems, however, that this can be accomplished in the case of many representatives of the American family Parulidae.

My attention was first drawn to these birds in the present connection nearly two decades ago. In considering the distributions in the Appalachian Mountains of various wood warblers, long and then still generally thought of as "typical" of northern coniferous forest, I came upon a statement by Brooks (1947:291, 295) remarking upon supposed changes in the habitat preferences of these species resulting from the destruction of virgin spruce in the Cheat Mountains of West Virginia. What an "amazing power of adaptation," Brooks mused in effect, was shown by those species able to give up "the traditional coniferous forests of their ancestors" and adapt, overnight as it were, to deciduous forest.

At the same time, however, in common with others, I (see Mengel, 1964) was finding some of the same species (for example Blackburnian, Black-throated Green, Black-throated Blue, and Canada Warblers) variously common in deciduous climaxes elsewhere in the Appalachians in places, such as the Cumberland Mountains of Kentucky, where spruce has not occurred in historic times, if ever (Braun, 1950:480). Considering this, together with the virtually certain origin of the Parulidae in the American tropics (Mayr, 1946: 21-22), it struck me forcefully that the true "ancestral homes" of these birds were obviously broad-leaved forests or related life forms and that coniferous forest was necessarily the secondary environment of those species capable of exploiting it.

When it occurred to me further that—because of certain peculiarities in the history of the North American continent—profound evolutionary opportunities would become available to the members of a tropical American forest-adapted group making this exploitation, the distributions and relationships of our northern wood warblers began to take on new significance.

Historical Background

It is essential to review briefly the Cenozoic history of North America. Readers familiar with this should skip this section. For further information, consultation of Flint (1957) on Pleistocene geology, King (1958) on Cenozoic history of the west, Dorf (1959) and MacGinitie (1958) on Cenozoic climates, Axelrod (1958) and Braun (1950, 1955) on vegetational history, Deevey (1949) and Martin (1958) on Pleistocene biogeography, and Kendeigh (1961: 280-339) for a very convenient summary of many pertinent details, should lead to practically all of a vast basic literature. The following capsule summary is based chiefly on the sources just cited.

Tertiary history.—At the beginning of the Tertiary (Paleocene, Eocene, Oligocene, Miocene, Pliocene) the climate of North America, then a continent of average low relief, was much more moderate than today's, with less marked alternation of seasons. Tropical and subtropical climates occurred far north of their present positions and were coextensive with a Neotropical-tertiary forest ancestral to today's tropical forests. North of this and continuously with Eurasia stretched a broad Arcto-tertiary forest consisting of a temperate (chiefly deciduous) element, much like the mixed mesophytic forests of Kentucky and Tennessee today, and a boreal element far to the north which, while richer in coniferous species, bore little resemblance to today's uniform northern coniferous biome. On the Mexican Plateau, probably in the Eocene, there first developed a mixed, woodland, Madro-tertiary flora (for map see Kendeigh, 1961:283, Figure 21-1).

Throughout the Tertiary, but from the Miocene especially, climate deteriorated rather steadily, while simultaneously the western cordilleran

mountain system was lifted to its present elevation or nearly so. With these changes:

(1) Floras and climatic zones were depressed southward, bringing the temperate Arcto-tertiary (ancestral deciduous) forest near its final level and driving the tropical forests into Central America.

(2) A broad rain shadow developed in the eastern lee of the rising mountains, forcing the temperate Arcto-tertiary forest eastward before newly developing grasslands and permanently isolating this forest from its Asiatic component and from a depauperate relict in the Pacific northwest.

The areas of the cooler, rising, and more arid west that were vacated by the temperate Arcto-tertiary forest were occupied, in the lower areas (and increasingly far northward), by various elements derived from the Madro-tertiary flora, while simultaneously the higher slopes were gradually colonized by boreal Arcto-tertiary elements. At some time, probably in the Miocene or Pliocene, a sclerophyll woodland and pine element of Madro-tertiary origin invaded the eastern Gulf States and southern Cumberland Plateau, and was ancestral to the southern pine-oak elements of the eastern deciduous forest.

There seems to have been, at the end of the Pliocene, still no real counterpart of today's extensive, uniform, northern and montane coniferous forest formations (Braun, 1950:511). These awaited Pleistocene glaciation for their fullest development.

Pleistocene history.—Gradually, approaching the close of the Pliocene, a long history of climatic deterioration (with increasingly sharp alternation of seasons), aided by mountain building, was culminated by the slow formation of continental and mountain glaciers of dramatic extent. In North America there is a clear record of four major glacial periods, the Nebraskan, Kansan, Illinoian, and Wisconsin (Figure 1). Between these occurred long, warm interglacial periods (Aftonian, Yarmouth, Sangamon) in which recession of ice and climatic amelioration equalled or exceeded today's (Figure 2). In these periods there must have occurred re-expansions of glacially displaced biota in patterns presumably similar to that which seems to have occurred after the last (Wisconsin) glaciation.

Two results of this recurrent glacial flow and ebb were particularly important in the present context.

(1) Upon glacial advance the boreal elements of the Arcto-tertiary forest were more or less separated by prongs of ice (facilitating their differentiation) and were forced far southward—to the Gulf coast, possibly, in the east, and deep into Mexico and Central America in the western mountains. In the southeast these boreal elements either mingled, or were forced into close proximity with, the somewhat compacted temperate (deciduous) Arcto-tertiary forest.

(2) Upon each glacial retreat there was probably established, although doubtless with increasing perfection in succeeding stages, a great, transcontinental, northern coniferous forest and (additionally) extensive montane coniferous forests in the west. This occurred, at least in part, as a result of the peculiar capacity of coniferous (especially spruce) forest rapidly and for a time exclusively to occupy recently glaciated terrain (Braun, 1950:521). Lacking this capacity, the complex remnant of the ancestral deciduous forest remained comparatively static, sending only depauperate "association-segregates" of beech-maple, oak-hickory, etc. (Braun, 1950:522) after the slowly retreating spruce.

Throughout, although varying in extent and position, the grasslands and

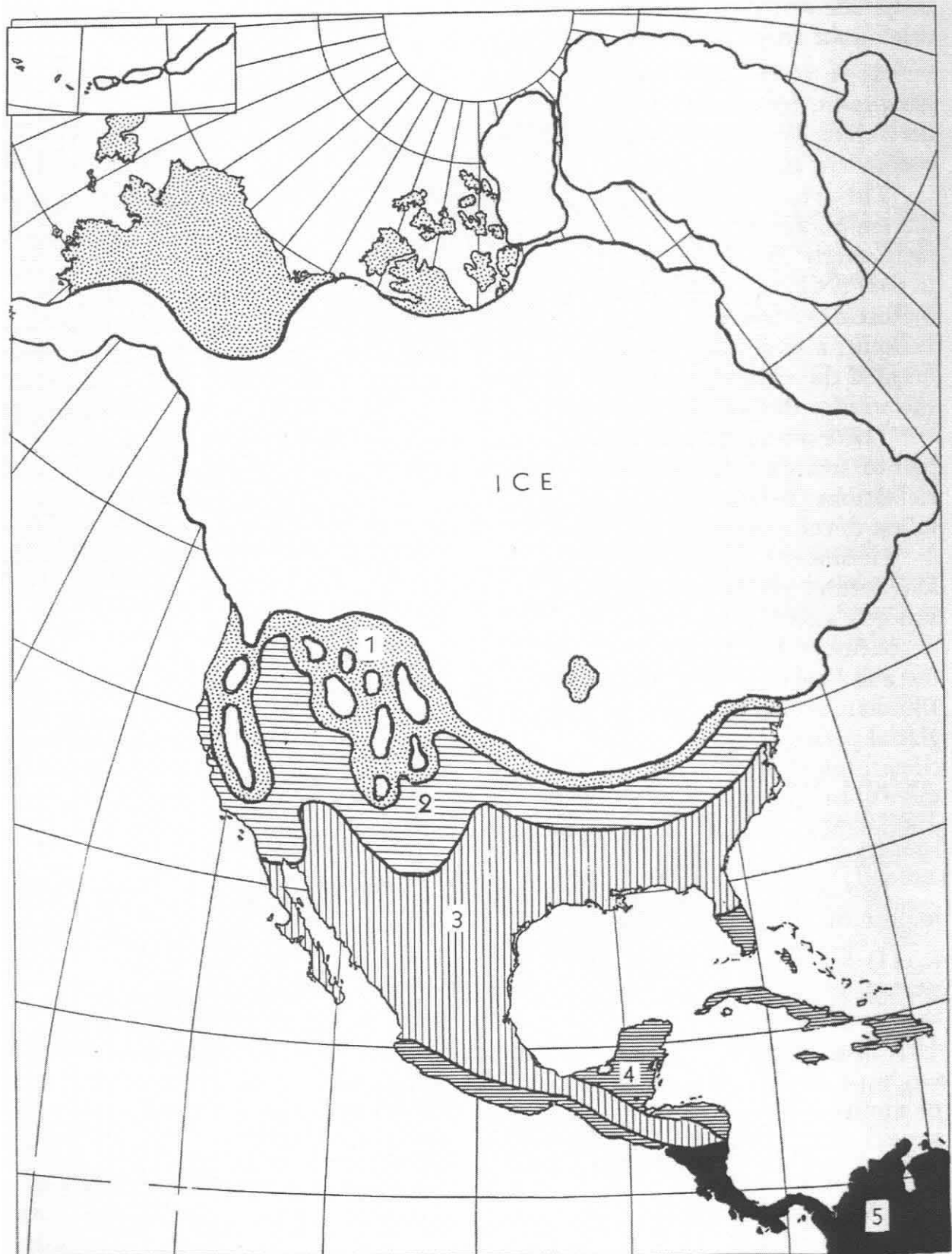


Figure 1. An approximate representation (modified from Dorf, 1959:195, map 5) of climatic conditions and glacial extent in periods of maximum Pleistocene glaciation in North America. The figure is a composite (no single glacier was so extensive, and the margin of each was irregular). The climatic zones are: 1, arctic (tundra); 2, subarctic; 3, temperate; 4, subtropical; 5, tropical.

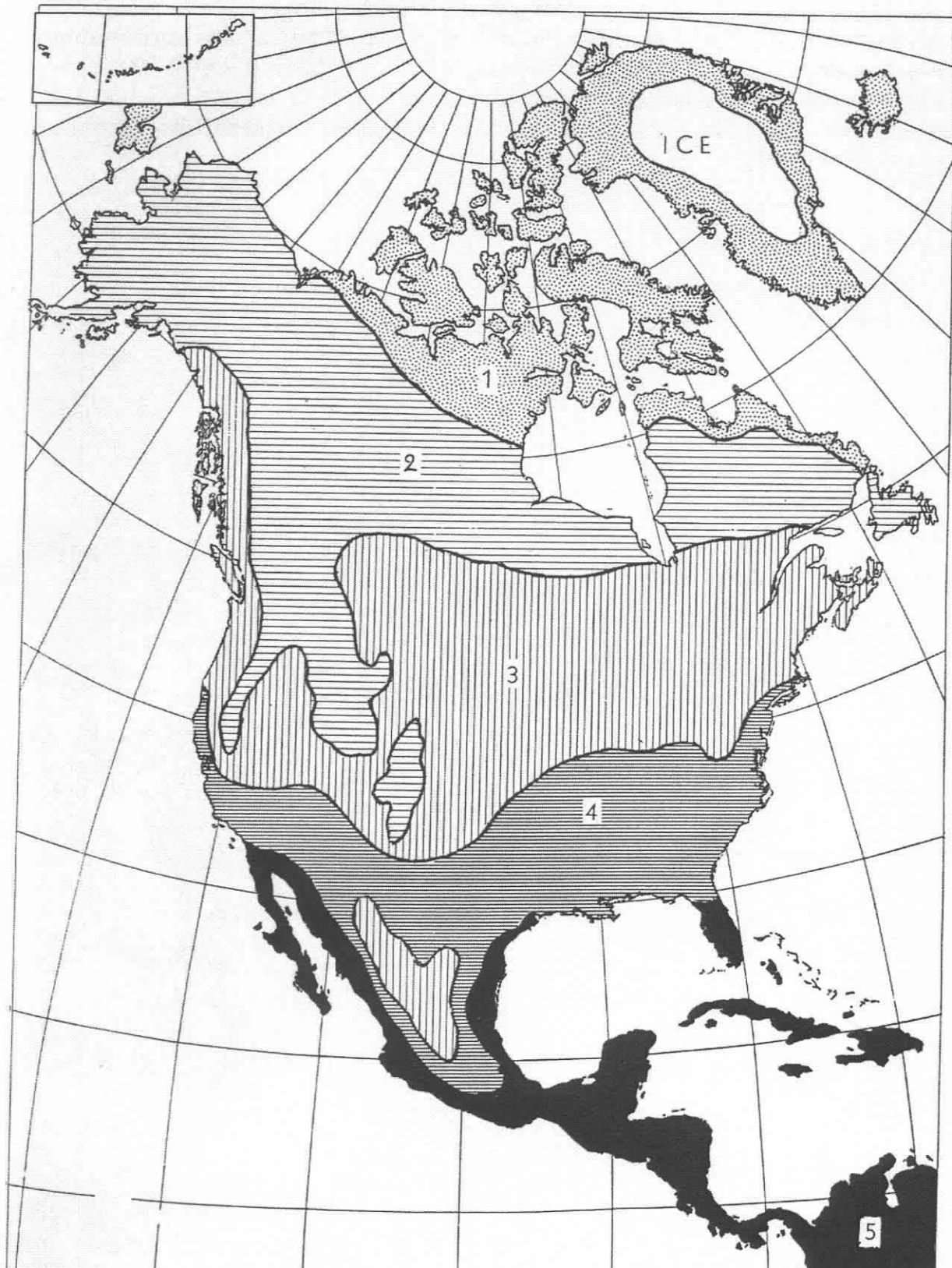


Figure 2. An approximate representation (modified from Dorf, 1959:197, map 6) of climatic conditions during the several interglacial climatic optima of the Pleistocene (save for the ice and the deep southward extent of northern conditions in the mountainous west, the map is also a fair representation of conditions in the late Pliocene; cf. Dorf, op. cit. :193, map 4). The climatic zones are: 1, arctic; 2, subarctic; 3, temperate; 4, subtropical; 5, tropical.

deserts maintained a gap between the deciduous forest of the southeast and the coniferous forests of the mountainous west.

Finally, in the warm, dry interglacials, the western mountain forests must have tended, as they do today, to retreat up the slopes, making forested "islands" of many of the separate mountain masses. Beneath and surrounding these coniferous forest islands were larger pine, oak, and scrub islands of Madro-tertiary origin, isolated from each other by seas of desert and grass. The ultimate disposition of the forest biomes developed through this history is shown in Figure 3.

A Model Sequence

We are now ready to examine the relationships between these events and the wood warblers. Let us begin by imagining a hypothetical ancestral species

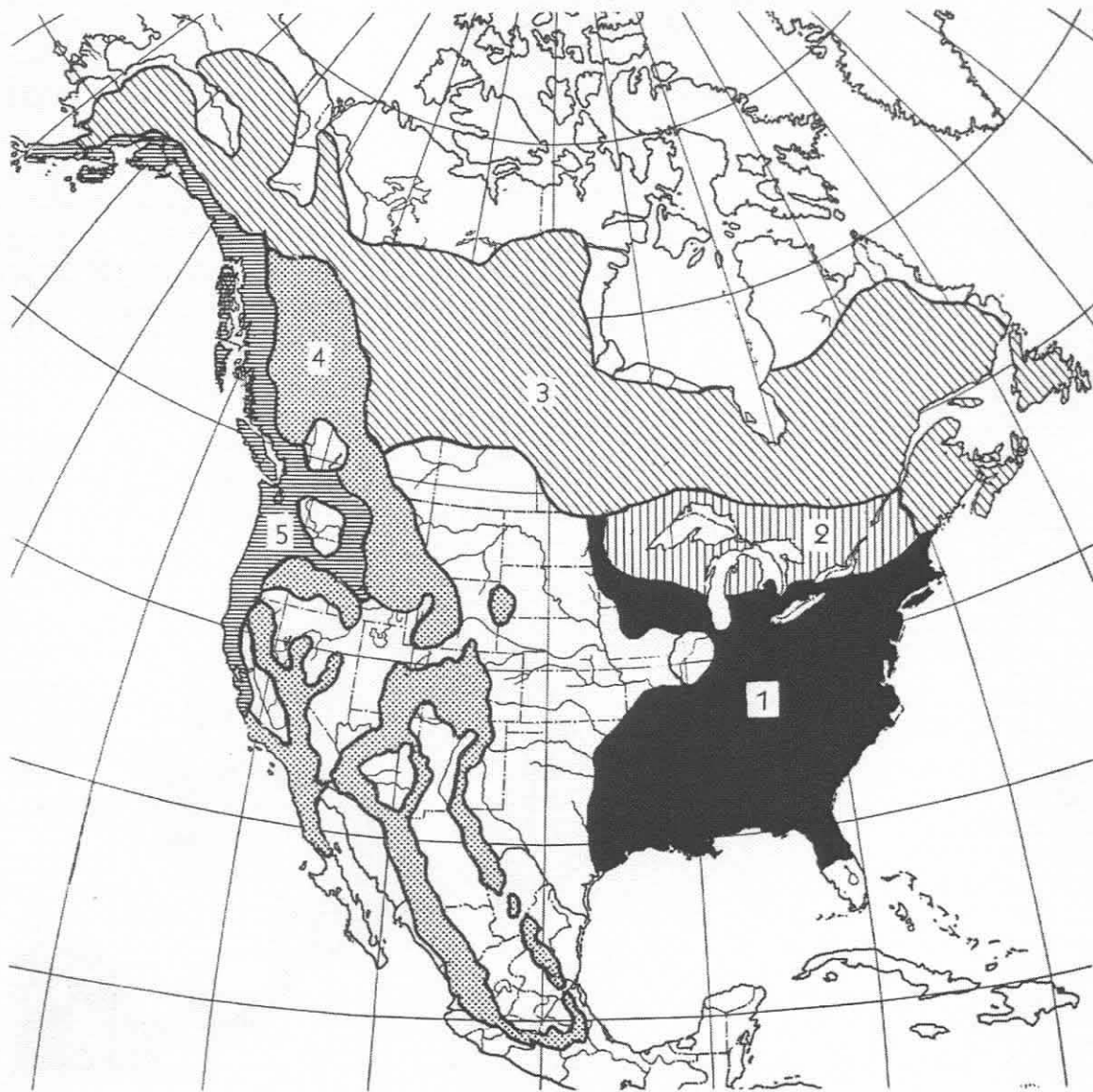


Figure 3. A rough representation of the major North American forest formations of today, modified from Weaver and Clements (1938:frontispiece). We may suppose the formations existing in previous interglacials (with Moreau, 1963:396, I regard distinction between Pleistocene and "Recent" as superfluous) to have been fairly similar. The forest types are: 1, eastern deciduous forest; 2, lake forest (an ecotonal mixed deciduous-coniferous forest); 3, northern coniferous forest (including taiga); 4, western montane (lower) and subalpine (higher) forests; 5, coast (chiefly coniferous) forest. In this paper types 4 and 5, collectively, are usually referred to only as "western montane forests."

of wood warbler adapted to the remnantal, deciduous, Arcto-tertiary forests of southeastern North America at the close of the Pliocene.

With the advent of the Pleistocene and the southward movement of Nebraskan ice, great changes must have occurred at the northern margins of the compacted deciduous forest and to a controversial depth within it. With these changes our ancestral parulid species would have been exposed, for the first time, to the boreal Arcto-tertiary (e.g., northern coniferous) forest elements forced southward by glacial ice. Whether or not, as Brooks conjectured (1947:294), bird populations were "compressed" in the southeastern refugium upon glacial maxima, with an ensuing theoretical increase in competitive pressures (this seems improbable), the ancestral parulid of our model was presented with the opportunity of making, or beginning to make, the adaptation to a completely new and potentially northern coniferous forest environment.

Now consider the advantages open to a species or population making this adaptation. Upon retreat of glacial ice and the subsequent establishment of coniferous forest in its place, this species would possess the key to *exclusive occupancy of a vast transcontinental range*. Our hypothetical warbler having accepted this opportunity, we have arrived at the situation shown in Figure 4, C.

This transcontinental distribution introduces a new and vital possibility, because the species is vulnerable to disjunction upon the next glacial advance (Figure 4, D). Geographical isolation would then be realized and differentiation could begin, not only in the refugia of the Nebraskan glaciation but continuing through the following warm interglacial—given isolation in western mountain forests then restricted to separate mountain masses (Figure 4, E).

At this point, moreover, the whole process could be repeated. That is, the original ancestral parulid (or, more properly, its modified descendant) during the Kansan maximum (Figure 4, D) would be renewing, perfecting, or maintaining its coniferous forest adaptations, and would again re-advance through the expanding coniferous forests of the second interglacial (Figure 4, E), again to achieve a transcontinental distribution and renewed vulnerability to disjunction.

It is unnecessary to follow the sequence to its logical conclusion as shown in Figure 4, F-I. If the process outlined be repeated successfully (that is, with differentiation to the species level in each case) through four glaciations and into the present fourth "interglacial," there would be one modified "parental" species in the east and three "derivative" species in the west (why four derivatives are shown in Figure 4, I, will become clear shortly).

There is, further, the possibility of additional derivative species being formed, if western differentiates should re-invade the northern coniferous forest (a possibility indicated by the dotted arrows of Figure 4), again to achieve a transcontinental distribution but from the opposite direction. This seems likely to have occurred, although rarely.

Analysis of Wood Warbler Distributions

A few preliminary remarks should precede consideration of concrete cases. Most importantly, it seems too much to expect that the descendants of any particular ancestral parulid would actually have pursued in full the precise course of the model, and, if they did, it is perhaps equally unlikely that all of

the resulting forms would survive. Various ancestors probably did not begin at the beginning of the course; others, so starting, did not successfully complete all stages; still others, running all or part of the course, may have left an imperfect record through extinction of descendants. And there is, finally, the excellent possibility that two or more derivative species sometimes resulted from isolated remnants of a single invasion.

Here also I must caution the reader against too ready acceptance of chronological indications. If, here and there, I suggest that two related events occurred in the Illinoian and Wisconsin times, respectively, what is more definitely indicated is only "earlier" and "later," such indications being based on an assumption (probably valid more often than not) that greater differences take longer to develop than lesser ones. Definite times are offered only as appealing possibilities.

These various qualifications do not detract from the instructive value of the model. Let us now turn to the living wood warblers in search of support for the hypothesis.

The Black-throated Green Warbler Group

This group (Plate I) is most intriguing in the present connection. It consists of five species of obviously very close relationship. Four of them, the Black-throated Green Warbler (*Dendroica virens*), Townsend's Warbler (*D. townsendi*), Hermit Warbler (*D. occidentalis*), and Golden-cheeked Warbler (*D. chrysoparia*), are extremely similar in many basic respects. High-ranging, high-nesting species of coniferous or partly coniferous forest, they are essentially allopatric and form a classical superspecies *sensu* Mayr (1942:169). The lower-nesting, lower-ranging Black-throated Gray Warbler (*D. nigrescens*) is smaller than the rest, slightly different in proportions and pigmentation, and somewhat aberrant ecologically; it is sympatric to some extent with *D. townsendi* and broadly sympatric with *D. occidentalis* (Figure 5).

A convenient summary of the habitat preferences of the group by Stein (1962) is brief but still more extensive than can be attempted here. This should be consulted, together with those general treatments (Griscom, Sprunt, et al., 1957; Bent, 1953; Chapman, 1907) which apply to all warbler species here discussed.

Since the remarkable similarity of the distributions of the group (Figure 5) with the terminal stage of the model (Figure 4, I) will probably be noted, I hasten to confess that Figure 4 was constructed precisely as it was for dramatic effect. If, however, the drama is diminished by the confession, inspection of Figure 6, showing the distribution of another species group, will reveal that nature has provided a sufficiently dramatic resemblance on her own!

The Black-throated Green Warbler.—This species has a wide range in the northern coniferous forest, the ecotonal lake forest, and the mixed forests of the Appalachian Mountains, where it tends to occupy various but rather circumscribed niches. Its present, nearly continent-wide distribution places it in jeopardy of disjunction upon another glacial advance. Although it no longer enjoys a very wide distribution in the eastern deciduous forest, there is evidence that it may once have done so, since it maintains marginal populations in cool, upland deciduous climaxes and extensive populations wherever hemlock is an important dominant of the mixed mesophytic forests. A morphologically poorly-marked race (*D. v. waynei*) occupies pure deciduous growth near the central Atlantic coast. Descent with modification from an

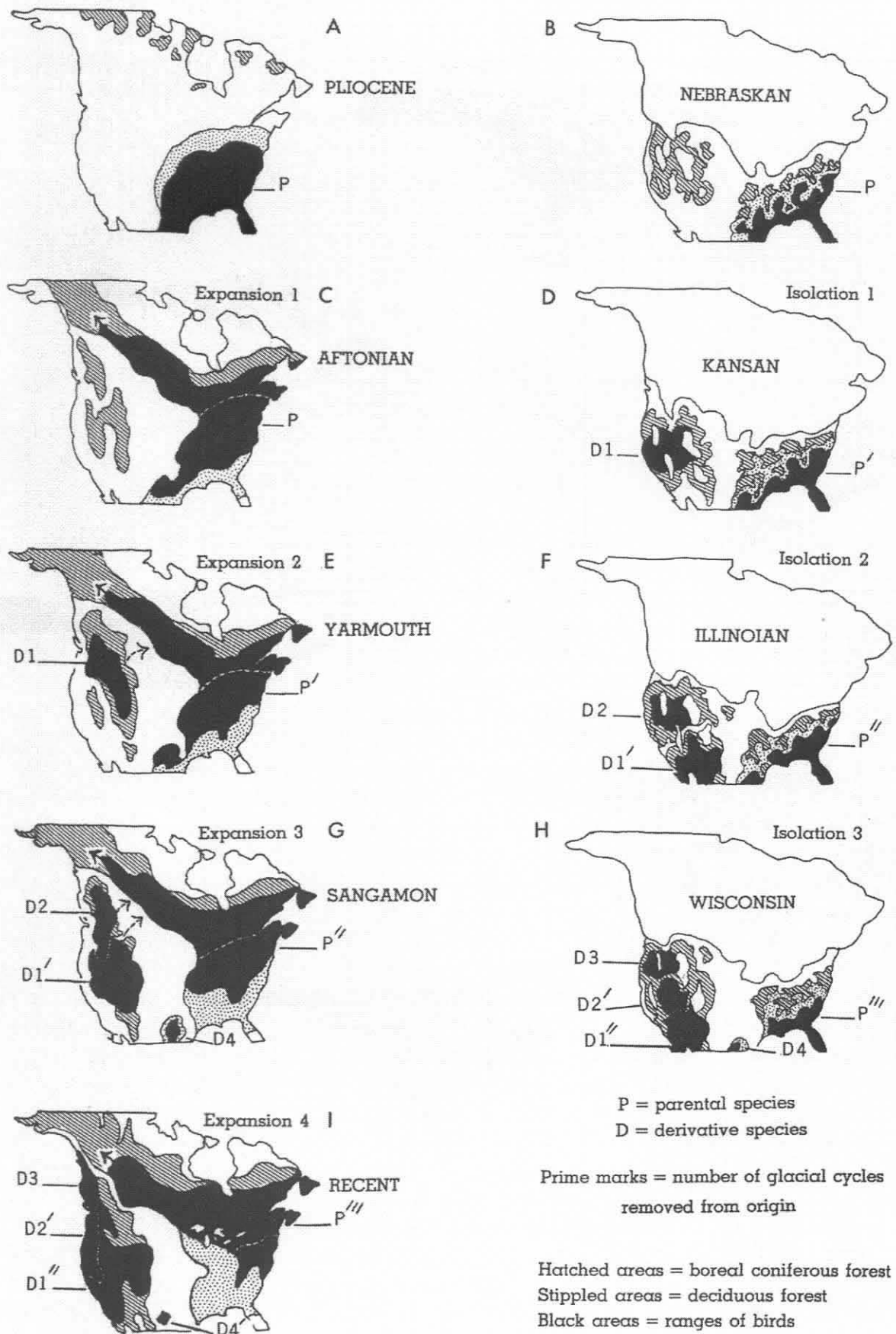


Figure 4. A model sequence showing the effects of glacial flow and ebb on the adaptation and evolution of a hypothetical ancestral wood warbler and its descendants (see text for explanation). The details of glacial boundaries are not meant to be accurate.

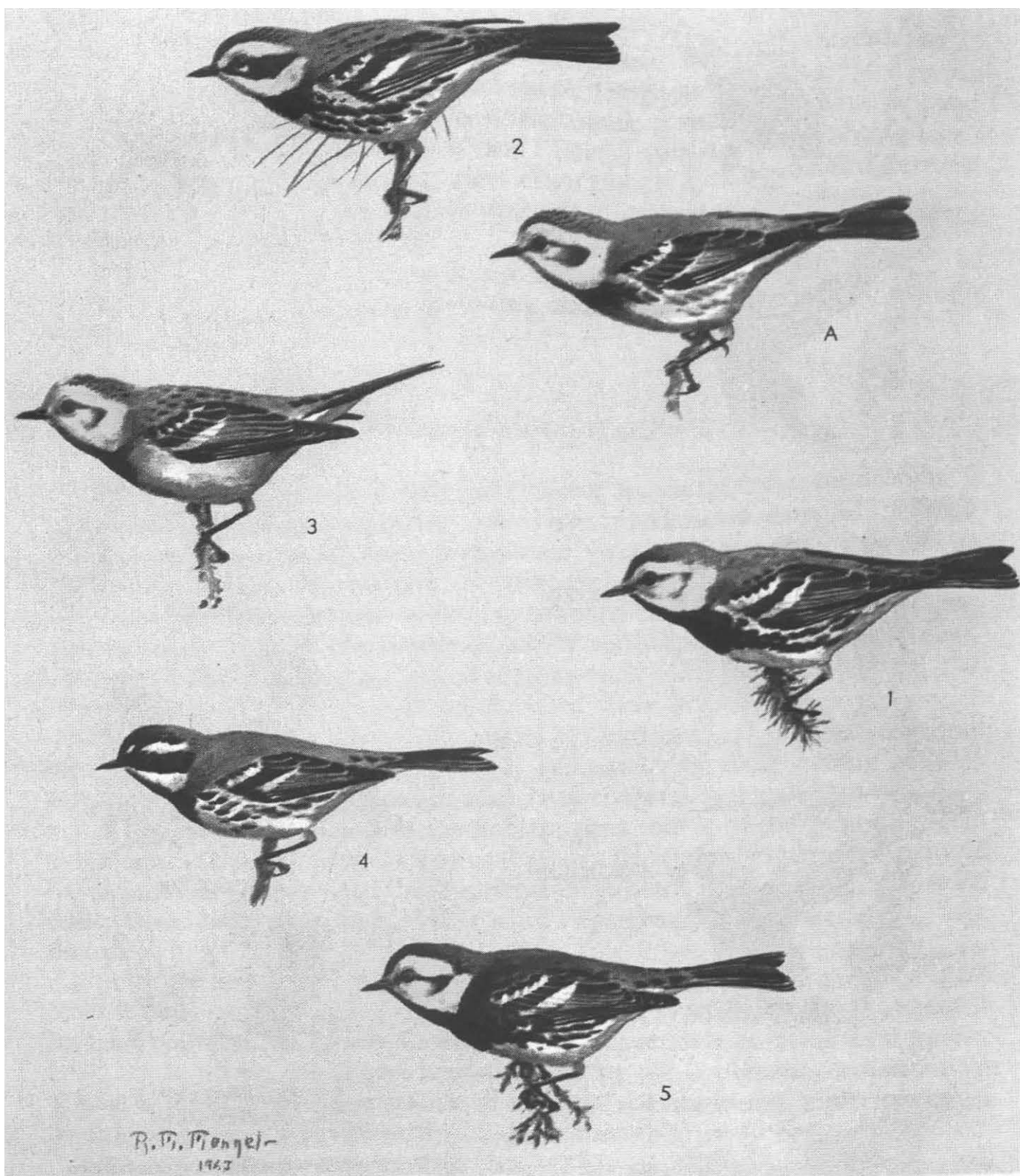


Plate I. The Black-throated Green Warbler Group

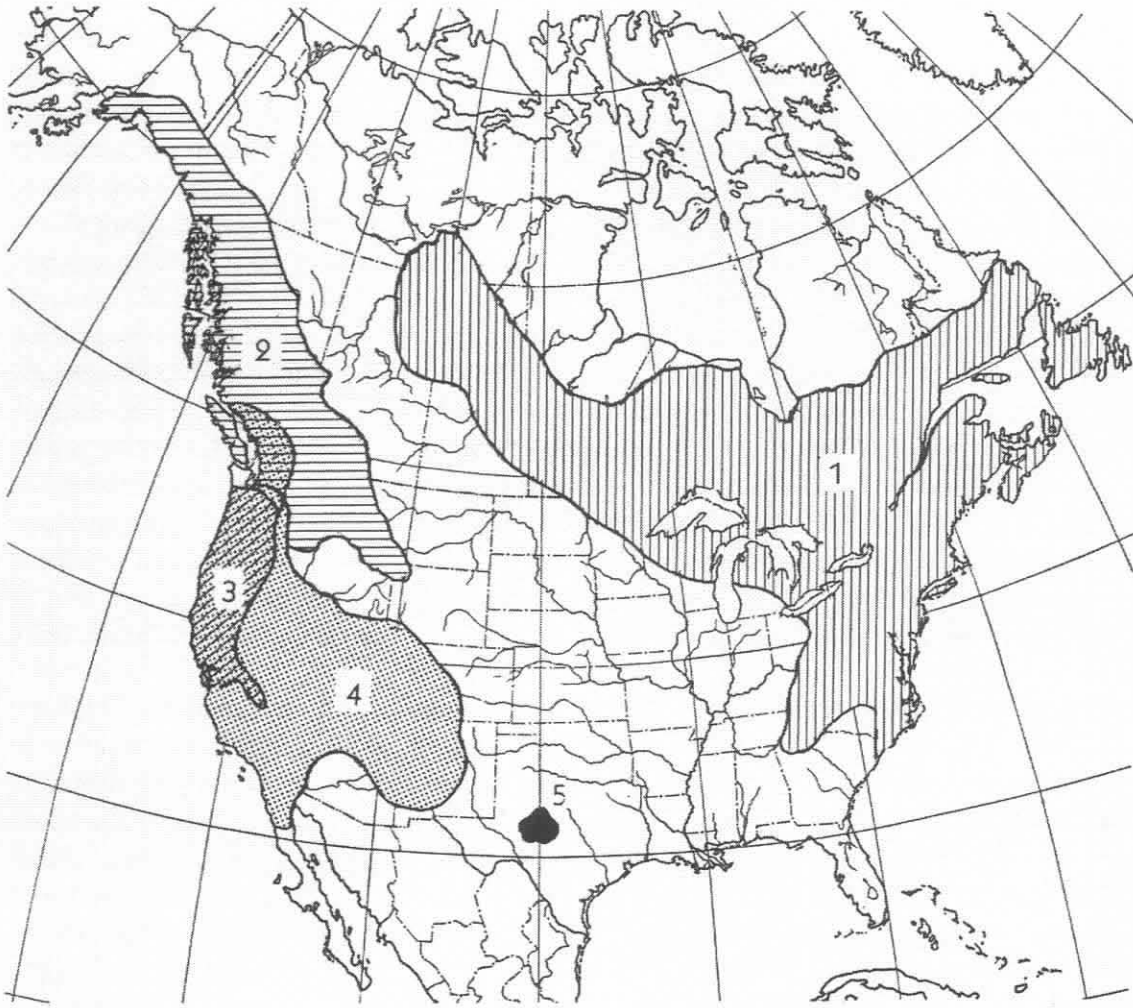


Figure 5. Approximate breeding distributions of the Black-throated Green Warbler group. 1, Black-throated Green Warbler; 2, Townsend's Warbler; 3, Hermit Warbler; 4, Black-throated Gray Warbler; 5, Golden-cheeked Warbler. The numbers and positional relationships of the ranges are reflected by those of the birds of Plate I (opposite) and will identify them, save for the extra bird of the plate (A), which is a hybrid Townsend's $\times$ Hermit Warbler. The birds are adult males in fresh to somewhat worn autumn plumage except the hybrid, which is a first-year male in the same plumage.

ancestor of long deciduous forest history (see also under Golden-winged Warbler) seems very likely, although in its present form the species has nearly relinquished its deciduous forest affiliations in favor of mixed and purely coniferous forests. Its song, appropriately for a species occurring sympatrically with many other wood warblers, is markedly stereotyped, although displaying two patterns (Stein, 1962:64).

The Townsend's Warbler.—This species occupies various specialized coniferous climaxes in the giant trees of the humid northwestern coast forests, and seems to have no overlap with the preceding species, although the gap (in Alberta) between their present breeding ranges is not great. Its similarity with the Black-throated Green Warbler is obvious (Plate I) and has been noted by many. The song, while differing in phraseology from that of the Black-throated Green (and more variable, befitting a species with few sympatric congeners) is still more similar to it in quality than those of the next two species (Stein, 1962:65). It seems very probable that Townsend's Warbler was derived from a western invasion of the ancestors of the Black-throated Green

Warbler (I shall henceforth use the prefix "pro"—e.g., in the present case "pro-*D. virens*"—to avoid the unwieldy "ancestors of the . . .").

The Hermit Warbler.—The last statement applies equally to this species, whose differences from the Black-throated Green, while slightly disparate in kind, are little if any greater in degree. The species, which occupies tall, coniferous Cascade and Sierra Nevadan montane forests (hence occurring at higher elevations than Townsend's Warbler), slightly approaches the Black-throated Gray Warbler in its diminution of xanthic pigments. Its song shows patterns difficult to distinguish both from the Townsend's Warbler on one hand and the Black-throated Gray on the other (Stein, 1962:68).

The Hermit Warbler may be an earlier differentiate than the Townsend's, but it is perhaps easier to conceive of the two as descending simultaneously from isolated differentiates resulting from the same western invasion of pro-*D. virens*. In either case their differences from each other and from the Black-throated Green Warbler suggest the possibility, if not the probability, of differentiation of one or both in a time earlier than Wisconsin, perhaps Illinoian. (This is indicated by comparison of their differences with those displayed by various species—or near-species—such as Audubon's and Myrtle Warblers, thought more clearly to represent very recent, probably Wisconsin, differentiation.)

Within their narrow zone of sympatry Hermit and Townsend's Warblers are known to hybridize (Jewett, 1944), and of several migrant hybrids taken in Arizona by Allan R. Phillips, one served as the model for the hybrid shown in Plate I, A. Although, as Jewett pointed out, various assortments of characters are shown by hybrids (possibly of second or later generations), at least some, like the one figured, interestingly display a combination of characters nearly reconstituting the Black-throated Green Warbler. This certainly suggests that various of the genes possessed by each are much like those of the Black-throated Green Warbler and tends to indicate a common ancestor much like that species.

The Black-throated Gray Warbler.—This comparatively minute species, nearly devoid of xanthic pigments but remarkably like Townsend's Warbler in pattern, enjoys a widespread distribution geographically overlapping both of the foregoing species but nearly if not quite separate ecologically. As Stein (1962:67) has summarized (from Chapman, 1907): "Its habitat in the northwest is mainly shrubby openings in coniferous forests, but elsewhere it varies from shrubby openings in mixed woods to dry slopes covered with oaks, junipers, and pinyon pine, and even chaparral." Relatively speaking, its geographic position, morphological differences (reduction in yellows, minute size), and addiction to comparatively xerophytic deciduous habitats are comparable to those of *Vermivora luciae* of the next group. It seems certainly to have descended from a western colonization more remote in time than that postulated for the Townsend's and Hermit Warblers. This may have been the colonization of an early pro-*D. virens* across an early northern route. Alternatively, its descent may be from a still earlier ancestor of Madro-tertiary affiliations which simultaneously or later gave rise to earliest pro-*D. virens* later to follow the northern route of the model. Its choice of habitat may suggest the second alternative, although, on the other side of the ledger, the early "northern routes" may have involved coniferous forests less highly evolved and less uniformly coniferous than today's.

In song also—"about the most variable and the least stylized" (Stein, 1962:68)—it seems to stand at the extreme with reference to the group at large.

The Golden-cheeked Warbler.—Like the Kirtland's and Colima Warblers, this species appears to be a relict and in danger of extinction. Its geographic position, on the Edwards Plateau of central Texas, is intriguing. Are these birds, as I once thought, the now restricted remnants of a once widespread early western differentiate? The song of the species, in which Stein (1962:67) detects resemblance to the Hermit Warbler (but which also suggests the Black-throated Green), might suggest this, but several considerations lead me now to think not.

First, the species seems to me strikingly like a somewhat melanistic Black-throated Green Warbler, an opinion shared by Lester L. Short, Jr. (letter, 29 August 1963), who has written me as follows: "*Dendroica chrysoparia* appears to be a strongly differentiated disjunct form of *D. virens*. . . . The Golden-cheeked Warbler sings very much like the Black-throated Green. . . . [the] characters of *chrysoparia* are observable to some extent in *virens*. Individuals of the latter may show considerable black on the back and crown. Young and even adult male *virens* frequently exhibit moderate to strong development of a transocular stripe. Finally, the race *waynei* of *D. virens* is similar to *chrysoparia* in having a more restricted black patch on the throat and breast."

Second, the distributional relationship between *D. virens* and *chrysoparia* is remarkably suggestive of a number of plant and animal distributions ably analyzed by Blair (1958), strongly indicated to be Wisconsin in origin, and thought to mark the presence on the Edwards Plateau of a postclimax relict of the eastern deciduous forest community.

This, with the bird's habitat—cedar brakes containing miscellaneous deciduous growth—seems to me to be evidence of an originally broad deciduous forest range of late pro-*D. virens* in the not-too-distant past. Whether or not this is so, a hypothetical pinching off of this relict species explains the presence of four (rather than the "expected" three) western differentiates in Figure 4, I.

Finally, the Golden-cheeked Warbler, unlike other members of the group, still migrates to a winter home largely coextensive with that of *Dendroica virens*.

Remarks.—This group, of all to be considered, has a conformation most closely resembling that of the "ideal" model, and in fact may have come fairly close to the "ideal" history. It appears to consist of an eastern form (*D. virens*), modified by long descent from an old deciduous forest ancestor (pro-*D. virens*); of a disjunct, relict descendant quite recently separated from the same ancestral line (*D. chrysoparia*); and of three western differentiates representing the descendants of (probably) one earlier (*D. nigrescens*) and one or two later (*D. townsendi*, *D. occidentalis*) western invasions, the latter two probably and the first possibly by pro-*D. virens*.

Earlier I (see Mengel, 1963:394) have indicated without discussion disagreement with Stein's conclusions (1962:69) that in this complex the Black-throated Gray is closest to Townsend's Warbler and the Townsend's and Black-throated Green and the Hermit and Golden-cheeked Warblers are "counterparts."

Although Stein seemed by the use of this word to imply descent from an immediate common ancestor, perhaps he meant only resemblance, rather than phylogenetic equality. His conclusions were based, in any event, as all such conclusions to some extent must be, upon resemblances, particularly between plumage patterns and song spectrograms (the significance of which is still little known). Evaluation of resemblances, of course, is largely subjective, and I have

already admitted to interpretative differences with Stein. I agree with Lester Short (letter) that "there is a great plasticity of color pattern in this warbler group, so that one can on this basis make a case for almost any arrangement of relationships among the various forms."

Still more importantly, I agree with Udvardy (1963:1147), that consideration of community histories and zoogeographic evidence—with their suggestions of the probable and the possible—must also be given significant weight in the evaluation of present conditions. It is comparatively difficult to reconcile Stein's suggestions with current indications of the biogeographic history of the late Cenozoic.

The Nashville Warbler Group

This group (Plate II) consists of four obviously closely related species, the Nashville Warbler (*Vermivora ruficapilla*), Virginia's Warbler (*V. virginiae*), Lucy's Warbler (*V. luciae*), and Colima Warbler (*V. crissalis*). Possibly the Nashville, Virginia's, and Colima Warblers should be thought of as a super-species, although this may strain the definition a bit. From this complex Lucy's Warbler stands apart in much the same ways as does the Black-throated Gray Warbler from the Black-throated Green complex, but somewhat more sharply.

The distributions of the group (Figure 6) are almost as striking in their apparent illustration of the theoretical model as those of the foregoing one, and the similarities stimulate the imagination. This group differs from the last in that its members are low-ranging, chiefly ground-nesting birds tending to inhabit shrubby deciduous seral stages in the coniferous forests and comparable shrubby situations elsewhere. A difference from the last group is that two *rac*es of the Nashville Warbler occupy geographic positions relatively (though not absolutely) comparable to those of two *species* (Black-throated Green and Townsend's Warblers) of the previous group. Each of the five forms, nonetheless, has a geographic counterpart in the last group.

The Nashville Warbler.—This species inhabits shrubby growth at the edges of deciduous, mixed, or coniferous forest. It retains a somewhat smaller present distribution within the northern part of the deciduous forest region than does the Black-throated Green Warbler of the last group, but its habitat preferences strongly suggest either an origin in the eastern deciduous forest region or a long history there. Two subspecies are recognized: *Vermivora ruficapilla ruficapilla* in the east and north, and *V. r. ridgwayi* (the "Calaveras" Warbler) with a fairly wide distribution in the mountains west of the Rockies. The latter utilizes various habitats of shrubby nature including chaparral, oak-scrub, piñon and juniper, and willows, sometimes at the edges of coniferous forest. The species stands in jeopardy of disjunction in case of further glaciation, even the eastern subspecies having a range sufficiently wide to make this a possibility.

The two races, which are not well differentiated, are unique among the unequivocal subspecies of wood warblers here considered in being separated by an (apparently) considerable gap extending from eastern Saskatchewan to central British Columbia. These facts suggest a wide western colonization, with subsequent imperfect or intermittent isolation of stocks, either in Sangamon time or (perhaps more probably) in very late Wisconsin time. The position of the present separation, in any case, and the slight distinction of the

forms, suggests that the disjunction may date only from the Valdres re-advance of Wisconsin ice some 11,000 years ago.

The Virginia's Warbler.—A somberly handsome little warbler, this one, like the foregoing, is a ground nester. It inhabits oak scrub (especially), oak mingled with pine, juniper, piñon, and similar communities at moderate elevations in the south-central Rocky Mountains and is essentially allopatric with *Vermivora ruficapilla ridgwayi*. Its choice of habitat is compatible with a descent from pro-*V. ruficapilla* ancestors of seral stages and edge situations like those occupied by the Nashville Warbler today. The song, as nearly as can be told from descriptions in the literature, is typically "Vermivoran" and not greatly unlike the Nashville's. The considerable distinctness of this species from the Nashville Warbler in various ways (I think greater than that of the Townsend's from the Black-throated Green Warbler) may suggest differentiation from a pro-*V. ruficapilla* of considerable remoteness, perhaps in Illinoian time. Marked resemblances to the Colima Warbler will be taken up under that species.

The Lucy's Warbler.—This is one of the most diminutive of wood warblers. In size and pallid coloration it exhibits superficial convergence with some of the bushtits, verdins, etc. of similar desert and semi-desert habitat. While it seems definitely to belong with the present group, it must be admitted that it is quite aberrant. Its plumage totally lacks xanthic pigments; its song (said to resemble a Yellow Warbler's) is distinctive; its rump, instead of the usual yellow, is chestnut like that of the striking Mexican species *Vermivora superciliosa*; and its choice of nest-sites (in crevices and cavities above ground) is unique. Additionally, it inhabits hot, dry desert regions in southwestern United States and northern Mexico that are home to no other wood warbler. These things place this species in the same relation to its group that the Black-throated Gray Warbler occupies in the preceding one.

Remote descent from a pro-*V. ruficapilla* crossing from the east by an early northern route is possible, but it seems equally if not more likely that this species descends from the isolated western population of an old, once widespread form of Madre-tertiary connections, whose eastern population became pro-*V. ruficapilla*.

The Colima Warbler.—A little-known species, this *Vermivora* is as remarkably large as Lucy's Warbler is small. Aside from size, its resemblance to Virginia's Warbler is marked. Its comparatively small breeding range is restricted, so far as known, to the Chisos Mountains of southwestern Texas and to mountainous parts of the Mexican states just to the south—Coahuila and Tamaulipas (probably), Michoacan and Colima (doubtfully). Its habitat and habits seem much like those of Virginia's Warbler, but its Pine Warbler-like song is distinctive. Its over-all morphological and ecological resemblance to Virginia's Warbler, however, suggests to me, as to Lester Short (letter), a close relationship and I think it likely that the two species stem from disjunct colonies from the same invasion of pro-*V. ruficapilla* in (probably) Illinoian time or earlier.

While the possibly coincidental but striking similarity of the distributions of the Colima and Golden-cheeked Warblers (Figure 5, 5; Figure 6, 5) tempts one to postulate similar origins, this seems unlikely, despite the recent sweeping pronouncement by Phillips (1962:364-365) that the Colima, Virginia's, and Nashville Warblers are conspecific. (In this connection I think the

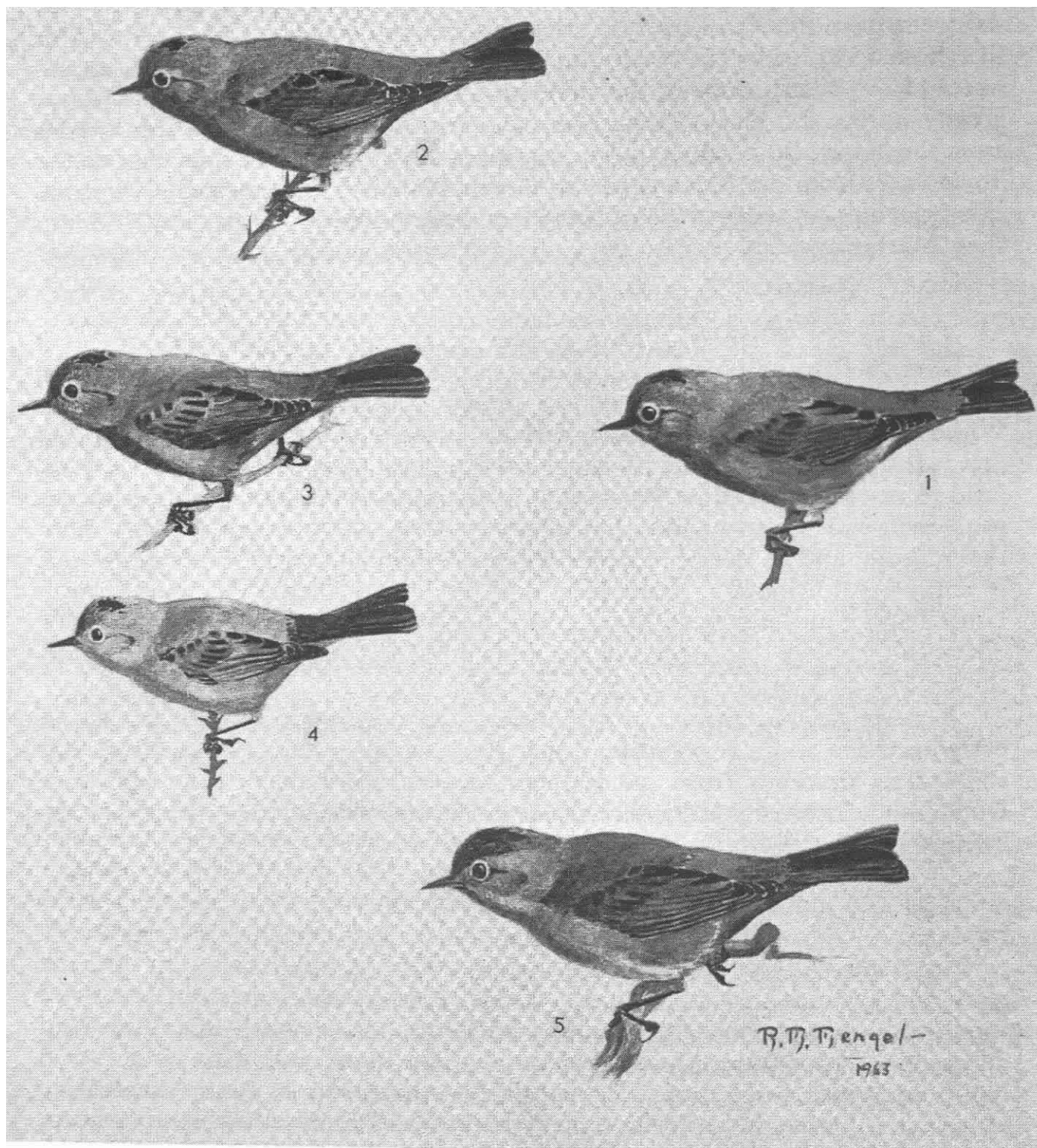


Plate II. The Nashville Warbler Group

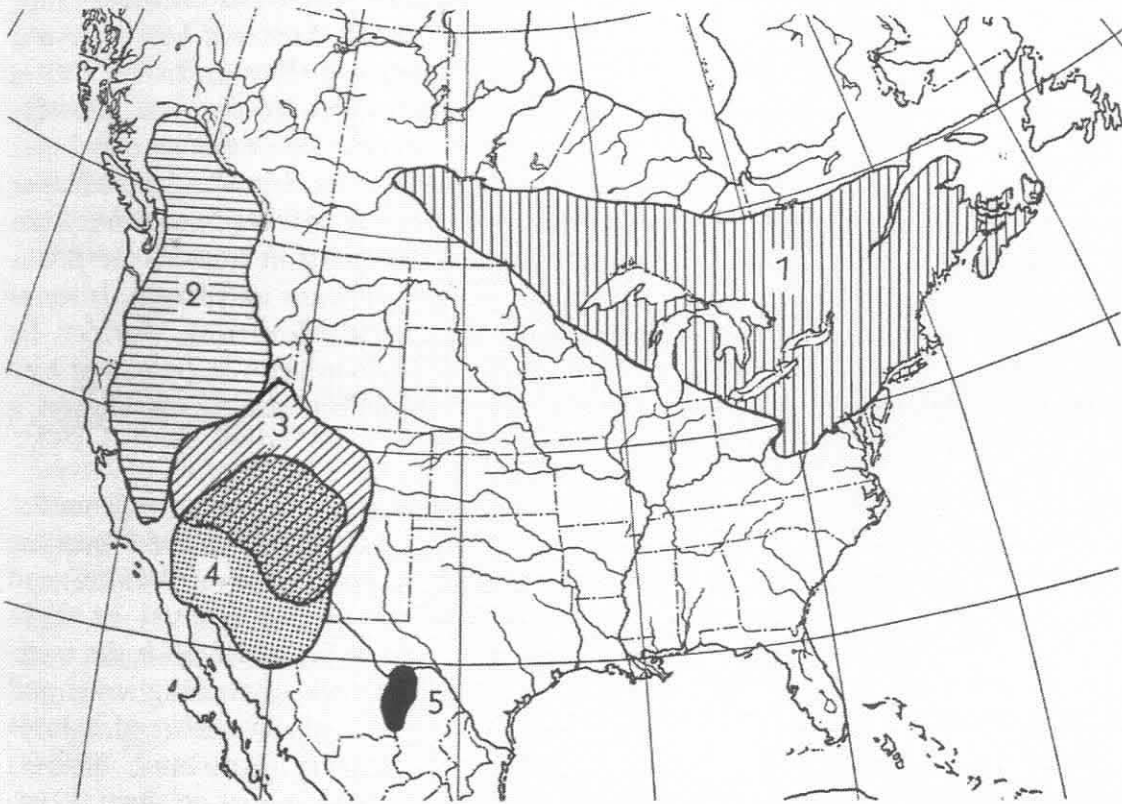


Figure 6. Approximate breeding distributions of the Nashville Warbler group. 1, eastern race of the Nashville Warbler; 2, western race of the Nashville Warbler; 3, Virginia's Warbler; 4, Lucy's Warbler; 5, Colima Warbler. The numbers and positional relationships of the ranges are reflected by those of the birds of Plate II (opposite) and will identify them. The birds are adult males in fresh autumn plumage.

statement of Mayr, 1942:170-171, concerning the value of the concept super-species should be strongly urged as relevant.) If Phillips' contention were valid, and if the Colima Warbler's origin were similar to that postulated above for the Golden-cheeked, I should expect to find both of them on the Edwards Plateau; to find considerably greater similarity between *V. crissalis* and *V. ruficapilla* than is evident to my eyes; and perhaps also to find *V. crissalis* performing a longer migration than it seems to, like most essentially eastern warblers and similar to that of *D. chrysoparia*.

The Connecticut Warbler Group

This group displays features which may be meaningfully interpreted in relation to the model, but which tax the power of imagination more than those of the foregoing groups. This is because the situation is probably "imperfect," in the sense of providing fewer species, or fewer surviving species, for analysis.

The group (Plate III) consists of only three species: the Connecticut Warbler (*Oporornis agilis*), which stands a bit apart, and the exceedingly similar Mourning Warbler (*O. philadelphia*) and MacGillivray's Warbler (*O. tolmiei*), which are doubtfully distinct at the species level but which, if so, form a superspecies. These are furtive, ground-nesting, low-ranging, large-eyed, long-legged birds adapted to gleaning foliage insects and turning leaves on the ground and in the low levels of the understory, in openings of mixed and coniferous forests. Their ranges are shown in Figure 7, A.

The Connecticut Warbler.—The oblong, rather restricted breeding range of the Connecticut Warbler is nearly central in North America, but extends a little more westward (northeastern British Columbia) than eastward (James Bay) in the northern coniferous forest. The species has, however, a markedly eastern migration route of great length, suggesting an eastern deciduous forest origin. It is questionable, considering its present distribution, whether it would be divided in the event of another glaciation or forced into an eastern or western refugium. Its distribution suggests that it is not now an ascendant species, and it may be on its way to reliction and ultimate extinction. It seems to be less numerous than the extensively sympatric Mourning Warbler. Its resemblance to the Mourning and MacGillivray's Warblers is great, but considerable differences in size, proportions, coloration, and song suggest a comparatively early divergence.

The MacGillivray's Warbler.—While differing in various ways from the Connecticut Warbler, this form is only dubiously distinct from the Mourning Warbler at the specific level, as already suggested by Phillips (1947:296) and Hofslund (1962:44). The morphological differences are limited to slight distinctions in size and coloration, the most conspicuous of which is the interrupted eye-ring of males, while behavioral differences, including song, and ecological differences are indeed slight so far as known. Two alleged hybrids considered by some to be evidence of limited sympatry (Hofslund, 1962:44) are of controversial identity as indicated in the original report on them (Peterson, 1958). In all, very recent differentiation is suggested.

The Mourning Warbler.—Almost restricted to edge situations in northeastern coniferous forests (south to West Virginia) and west in the north to Alberta, this is scarcely more than an eastern MacGillivray's Warbler. It has been claimed (Hofslund, 1962:44) that in song and perhaps other characters the Mourning Warbler shows increasing convergence with MacGillivray's Warbler as it approaches that form in the west. This is reminiscent of comparable convergence found in the sibling species of the meadowlarks *Sturnella magna* and *neglecta* (Lanyon, 1962:189).

Remarks.—I propose as a hypothesis that a pro-*O. agilis* stock originally derived in the eastern deciduous forest (where a congener, the quite distinct *Oporornis formosus*, the Kentucky Warbler, is still exclusively found), and gradually adapting to seral stages of the northern coniferous forest, early (perhaps in the Yarmouth interglacial, if not before) accomplished an invasion of the western mountain forests. It was disjuncted by subsequent glaciation, and differentiated into two forms, the western one of which was pro-*O. tolmiei*. While pro-*O. agilis* was losing its roots in the deciduous forest, pro-*O. tolmiei* differentiated fully and (I propose tentatively in Sangamon interglacial time) successfully accomplished a reverse invasion of the northern coniferous forest. This is suggested by the very large western range and geographic differentiation of several races within this range (Phillips, 1947) of *O. tolmiei* (the 1957 A.O.U. Check-list recognizes only subspecies *tolmiei* and *monticola*). Wisconsin glaciation, driving a wedge through this re-expanded range, permitted the isolation and comparatively slight differentiation resulting in the present, variable, western *O. tolmiei* and the homogeneous, eastern *O. philadelphia*. The migration route of the Mourning Warbler, more westerly and shorter than that of the Connecticut and to a winter range partly coextensive with that of MacGillivray's Warbler, may be further evidence of the origin here suggested for the Mourning Warbler.

Any alternative explanation seems to require more assumptions. The most obvious one would require the presence in the original eastern deciduous forest of both pro-*O. agilis* and pro-*O. philadelphia* (with no clue as to their differentiation from a common stock), and would further require us to assume that the ancestors of the form that is now most exclusively restricted to northern coniferous forest (*O. agilis*) never accomplished a sufficiently extensive westward colonization therein to permit isolation by glaciation (as evidenced, anyway, by a surviving differentiate).

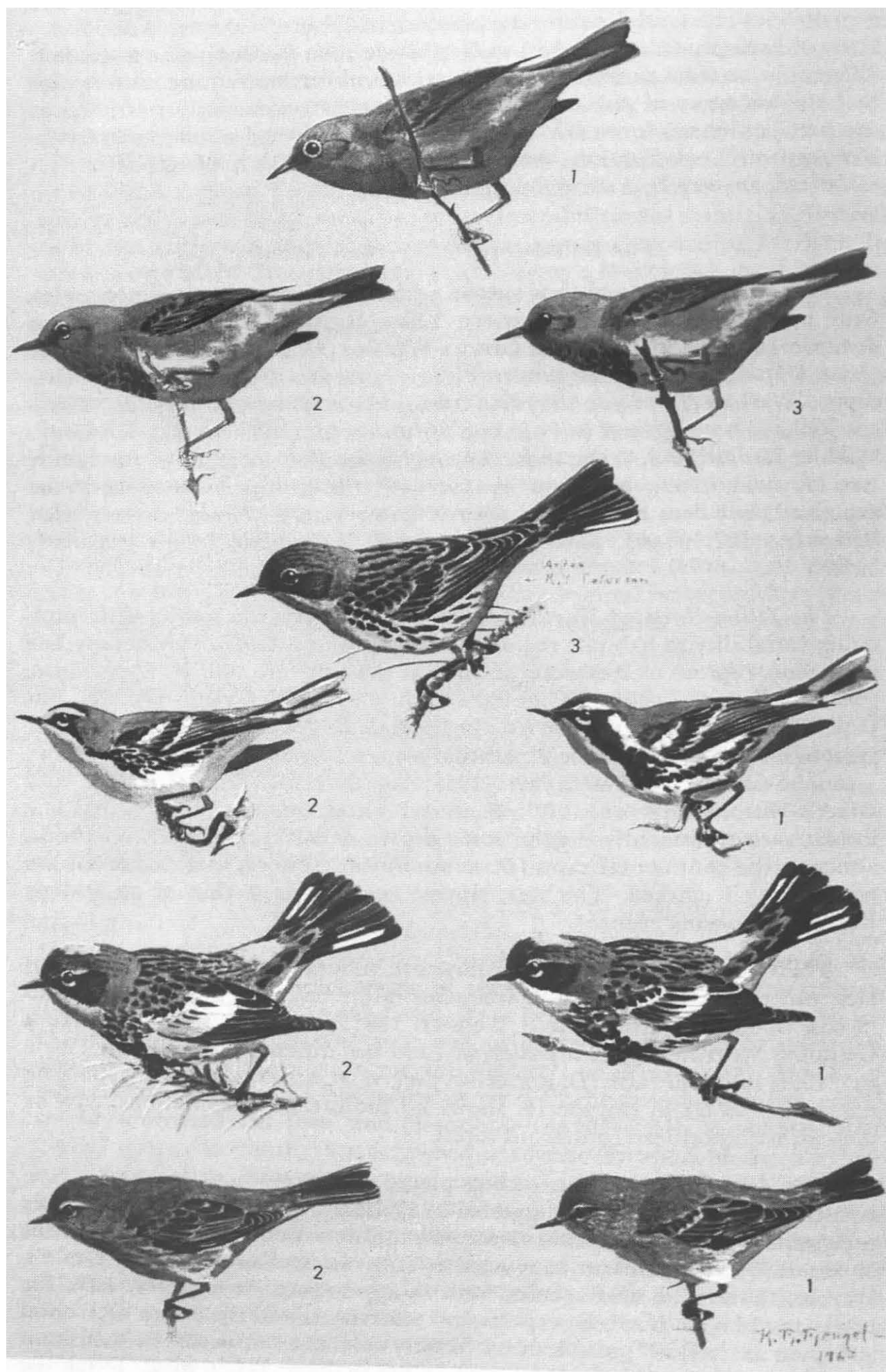
The Yellow-throated Warbler Group

This group consists of four species which may constitute a superspecies. Only two of them, the southeastern Yellow-throated Warbler (*Dendroica dominica*) and the southwestern Grace's Warbler (*D. graciae*) are figured here (Plate III). Completing the group (Figure 7, B) are the West Indian Olive-capped Warbler (*D. pityophila*) and Adelaide's Warbler (*D. adalaidi*). These species have been figured in Griscom, Sprunt et al. (1957: pl. 32). Kirtland's Warbler (*D. kirtlandii*), the most thoroughly studied member of the family (see Mayfield, 1960), has been figured with the group, for reasons to be explained, but does not belong with it immediately. (Note, however, that Ridgway, 1902:603-605, placed it next to *D. pityophila* in his systematic order.)

The Yellow-throated Warbler.—This is a southeastern species with interesting variability in habitat; regionally it may almost exclusively occupy live oaks, pine, cypress, or sycamore, so long as the trees are tall. Its appearance, general habits, and choice of habitat clearly ally it with Grace's Warbler, but the differences between the two (in song, size, details of pattern) are sufficiently great to make pre-Pleistocene separation seem reasonably probable. Certainly I cannot concur with Hellmayr (1935:400) that the Yellow-throated and Grace's Warblers are probably conspecific. Three continental races and one insular race additionally suggest some degree of antiquity for *D. dominica*, although the continental races (*D. d. dominica*, *albilora*, and *stoddardi*) are not very well marked. The soft, slurred song suggests that of an Indigo Bunting (*Passerina cyanea*).

The Grace's Warbler.—A southwestern mountain species, Grace's Warbler reaches Central America. It frequents tall pines, both in pure stands and in oak woodland (Phillips and Webster, 1961:551), sings something like a Chipping Sparrow (*Spizella passerina*), and has differentiated slightly (Webster, 1961) into four races (*D. g. graciae*, *yaegeri*, *remota*, and *decora*). Ranging north only to Utah, the species shows no indication of affiliations, past or present, with northern coniferous forest.

The Adelaide's Warbler.—Long placed next to Grace's Warbler in systematic lists, the species was suggested by Hellmayr (1935:400) to be probably conspecific with it, an extreme view in my opinion. Bond (in Griscom, Sprunt et al., 1957:265) seems to suggest that it is more disparate from Grace's Warbler than is the next species, both in appearance ("completely lacks the black streaking on both upperparts and underparts and the entire breast and abdomen are yellow") and habitat (mostly thickets, but occurs in mountain forests and tall trees on St. Lucia), although perhaps not in song. To me the combinations of characters displayed by the Adelaide's and Olive-capped Warblers, in comparison with Grace's Warbler, suggests the comparison of



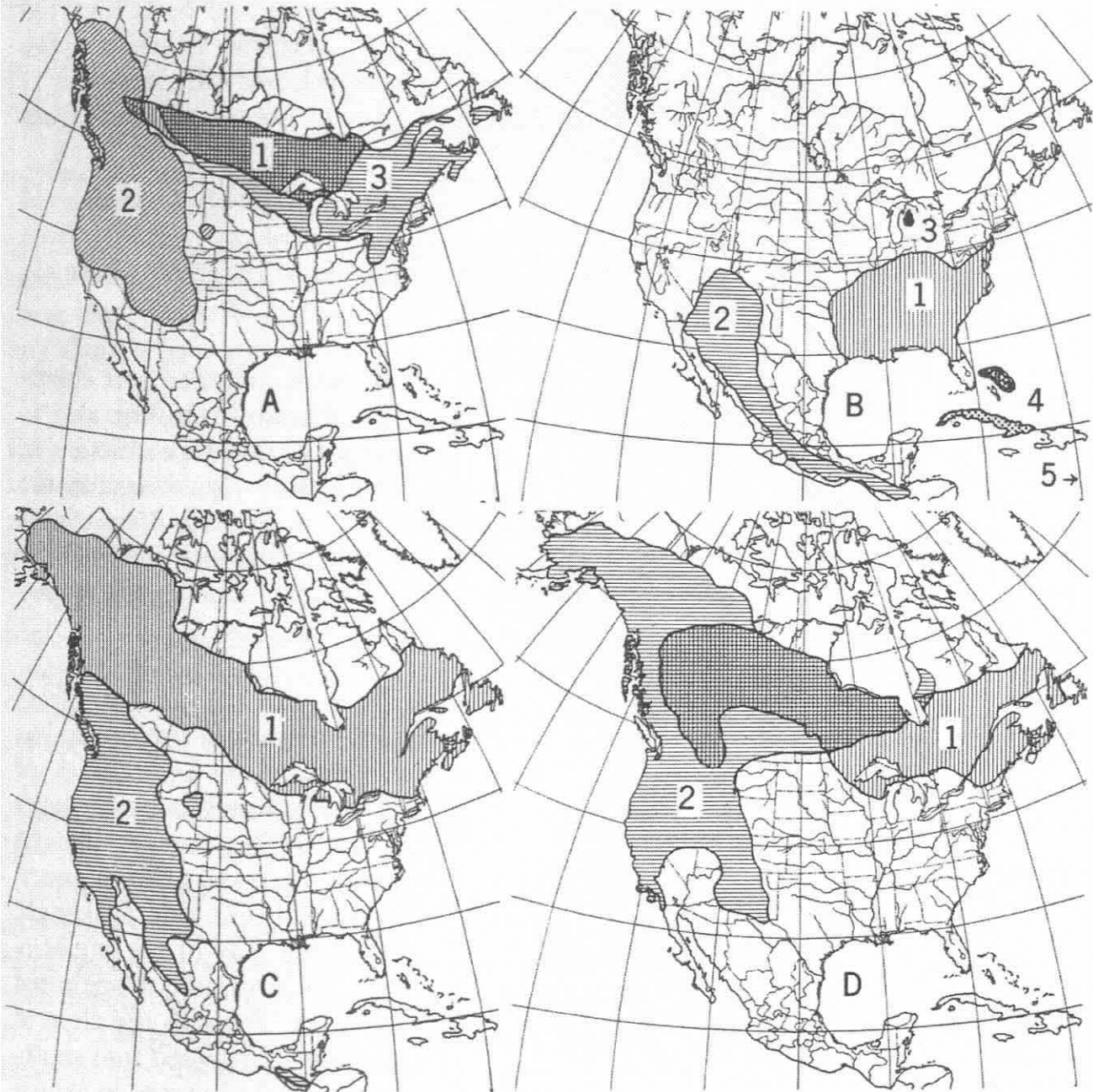


Figure 7. Approximate breeding distributions of the four warbler groups shown on Plate III (opposite). The numbers and positional relationships of the ranges are reflected by those of the birds in the plate and will identify them. A. Connecticut Warbler group (top three birds): 1, Connecticut Warbler; 2, MacGillivray's Warbler; 3, Mourning Warbler. B. Yellow-throated Warbler group (part) and Kirtland's Warbler (next three birds): 1, Yellow-throated Warbler; 2, Grace's Warbler; 3, Kirtland's Warbler (see text). The West Indian Olive-capped Warbler (4) and Adelaide's Warbler (5) are not figured. C. Myrtle Warbler group (next two birds): 1, Myrtle Warbler; 2, Audubon's Warbler. D. Tennessee Warbler group (bottom two birds): 1, Tennessee Warbler; 2, Orange-crowned Warbler. The birds are males in fresh autumn plumage, except for Kirtland's and Yellow-throated Warblers which are in somewhat worn breeding dress.

Townsend's and Hermit Warblers in their relationship with the Black-throated Green. The existence of three races in the present species suggests considerable duration of residence in the West Indies.

The Olive-capped Warbler.—This species, which differs from Grace's Warbler largely "by having a yellowish olive-green crown and by lacking the conspicuous black streaks on the sides and flanks" likewise inhabits pines, although at intermediate instead of upper strata (Bond, loc. cit.). As nearly as I can tell from Bond's written accounts, its song is not greatly different from that of Grace's Warbler.

It is perhaps worth noting that this species has probably been derived from its mainland ancestor in much the same way as *Dendroica vitellina* from the Prairie Warbler, another alleged member (Kendeigh, 1961:298) of the old Madro-tertiary sclerophyllous woodland assemblage.

[*The Kirtland's Warbler.*—This celebrated species is included here chiefly because of its interest, and its strikingly relictual distribution, but also to mention that both its appearance and its habitat (jack-pine reproduction in burned areas) suggest it may be a remnant of an ancestor also related to the old Madro-tertiary sclerophyll woodland element. Its West Indian winter range, in the Bahamas, is reminiscent of those of other species thought (Kendeigh, 1961) to belong with this element, e.g., Prairie, Pine, and Yellow-throated Warblers.]

Remarks.—Although the distributions of *D. dominica* and *D. graciae* might at first suggest it, there is little doubt that the history of this group has slight resemblance to that of the model. This is evidenced by the lack of adaptation of any of the forms to northern coniferous forest or seral stages thereof, and by their generally southern present distributions. Rather, it seems likely that the members of this group have been part of a fauna associated with vegetational elements—sclerophyll woodland, etc. (see Kendeigh, 1961:298)—derived from the Madro-tertiary flora, which may in the late Miocene and early Pliocene have been more or less continuously distributed around the Gulf of Mexico (see Pitelka, 1951:383-384). Towards the close of the Tertiary, this flora (with its attendant animals) was disjuncted into southeastern and western components by a combination of influences in which climatic change and expanding grassland were evidently predominant.

Thus an ancestral pine or pine-oak woodland parulid probably differentiated into two forms, pro-*D. dominica* and pro-*D. graciae*. Further multiplication of species was permitted when members of the ancestral form (doubtless isolated migrants or strays remaining to establish breeding populations; see Bond, 1948:208-210) became established at least twice in the West Indies and differentiated in truly insular isolation. Thus in Puerto Rico, Vieques Island, Barbuda, and St. Lucia, Adelaide's Warbler occurs today, with the Olive-capped Warbler occupying Cuba and the northern Bahamas (Grand Bahama, Abaco), in the latter of which it is sympatric with a well-marked, presently-differentiating race (*D. dominica flavesceus*) of the Yellow-throated Warbler. Interestingly, both West Indian species rather more resemble the geographically remote Grace's Warbler than the proximal Yellow-throated Warbler (Bond, loc. cit.), so that the ancestral form was perhaps rather more like Grace's Warbler than like the Yellow-throated. This seems also to indicate considerable, probably pre-Pleistocene, antiquity of the insular forms.

The Myrtle Warbler Group

The two species of this group (Plate III), the Myrtle Warbler (*Dendroica coronata*) and Audubon's Warbler (*D. auduboni*), if truly distinct as species, form a superspecies and seem to represent a recent differentiation, probably in Wisconsin time. Hybridization seems to be frequent (Packard, 1945; Alexander, 1945; and others), probably in a narrow zone of sympatry in British Columbia or Alaska.

The Myrtle Warbler.—Fully adapted to northern coniferous forest, this species has virtually no roots in the eastern deciduous forest. Its currently broad distribution places it in clear danger of disjunction in case of further glaciation. The northwestern population (*D. c. hooveri*) constitutes a poorly marked race, doubtless of post-Wisconsin differentiation. Like the following form, the Myrtle Warbler is remarkable in the family for its cold-hardiness and short migrations, wintering almost wholly in warm-temperate latitudes.

The Audubon's Warbler.—Much like the Myrtle Warbler, this mountain form occupies a very wide range from southeastern Alaska to Guatemala in western montane coniferous forests, where it has differentiated into four rather well-marked races (*D. a. auduboni*, *memorabilis*, *nigrifrons*, and *goldmani*).

In standard references the breeding range of the species is still given as south only to southern Durango. There is, however, a well-marked race, *D. a. goldmani* Nelson, breeding in the mountains of Guatemala and possibly Chiapas (van Rossem, 1934:402-403; Phillips, 1960:352; K. C. Parkes, pers. com.).

Remarks.—The history of the evolution of these two forms seems likely to be similar to that of the model, but only a fragmentary record exists.

The full adaptation of the two forms to coniferous forest, the absence of any remnantal deciduous forest affiliations of the Myrtle Warbler in the east, the absence of any clear relatives there, and the wide western distribution and considerable geographic variability of Audubon's Warbler all combine to suggest a long history largely obscured by extinction of critical forms. Two tentative hypotheses seem possible.

(1) The Myrtle Warbler descends directly from an eastern ancestor (pro-*D. coronata*) of early and long coniferous forest adaptations, whose deciduous forest affiliations were abandoned some time in the past. The Audubon's Warbler descends from a western differentiate resulting from the last western expansion of pro-*D. coronata*, the earlier differentiates that ought to exist either (a) having become extinct or (b) never having achieved full specific status (which seems less probable). Arguing against this hypothesis are the unique cold-hardiness and short migrations of the two forms, which qualities set the Myrtle Warbler sharply off from other eastern parulids.

(2) The Audubon's Warbler descends from an early differentiate resulting from the western invasion of an eastern ancestor now extinct, while the Myrtle Warbler is a recent (Wisconsin) differentiate resulting from eastward re-expansion of this pro-*D. auduboni*. In this case, it is not inconceivable that something much like today's Magnolia Warbler (adapted to northeastern mixed and coniferous forests) was the chronologically remote eastern ancestor. I favor the second hypothesis.

The Tennessee Warbler Group

Here, again, we have only two species (Plate III; Figure 7, D), the Tennessee Warbler (*Vermivora peregrina*) and Orange-crowned Warbler (*V. celata*) which, while clearly close relatives, are distinct well beyond the point of representing a superspecies (a possibility also precluded by their partial sympatry).

The Tennessee Warbler.—Thoroughly adapted to northern coniferous forest, the Tennessee Warbler, while breeding on the ground in *Vermivora* fashion, forages in the middle layers. Its staccato song is much like the Orange-crowned's but more emphatic and definite in form. It retains no appreciable connections in the eastern deciduous forest but its extremely long, presumably conservative, eastern migration route suggests a long eastern history. It shows no tendency toward geographic differentiation. Today, with its broad northern distribution, the species is in position to be disjuncted by subsequent glaciation. While it differs from the Orange-crowned in possessing a breeding dress modestly altered from the plumage assumed in autumn, the two birds in the latter plumage are remarkably similar. They differ slightly in proportions, the Orange-crowned having a relatively shorter wing and longer tail (appropriate to its much shorter migration). The Tennessee, unlike the Orange-crowned, lacks the orange patch typical of many of the genus.

The Orange-crowned Warbler.—In contrast to the Tennessee Warbler, this species inhabits brush and shrubby seral stages, sometimes riparian, in coniferous or mixed forest regions. A low ranger and, usually, a ground nester (occasionally nests in small trees up to 15 feet), it has a wide western range with four moderately distinct subspecies (*V. c. celata* in the north, east of Alaska and British Columbia; *V. c. lutescens*, *orestora*, and *sordida* in the west), suggesting a comparatively long western tenure. Eastward in the northern coniferous forest the species appears to be re-invading and has reached around James Bay. A western origin of these northern birds seems to be indicated not only by their distribution but also by their migration pattern (rather misleadingly stated by Bent, 1953:89). While some *Vermivora celata celata* do migrate through the east to winter homes in the Gulf States, as Bent says, they are a trickle in comparison with the flow that passes through the central and western states—here in Kansas, where I write, they are probably the most numerous migrant wood warbler—to winter in the southwest, Mexico, and Central America. In the north the species is broadly sympatric with the Tennessee Warbler.

Remarks.—No forms exist to suggest an early history relating the present group to the somewhat similar Nashville Warbler group. Neither are there enough species to permit a strong hypothetical reconstruction of past events. Nevertheless, the two species again recall the model.

Since their considerable differences suggest some remoteness of differentiation, I suggest that pro-*V. peregrina* early, perhaps in Yarmouth time, established by way of northern forests a western stock which upon isolation by Illinoian glaciation differentiated into pro-*V. celata*. *V. celata* now, perhaps for the first time, is accomplishing a re-invasion of the northern coniferous forest that is already sufficiently extensive to permit isolation by glaciation.

Any additional derivative species have been lost by extinction.

Other Northern Wood Warblers

A few species should be mentioned whose present distributions, adaptations, and similarities, while suggesting very little when the birds are considered singly, may assume some significance in light of all that has been said here.

There are morphological, behavioral, and ecological similarities between the Blackpoll Warbler (*Dendroica striata*), Bay-breasted Warbler (*D. castanea*), and Cape May Warbler (*D. tigrina*) that suggest they may be quite closely related (the resemblance, particularly of the first two, in autumn plumages is well known to banders, bird watchers, and others), and a hybrid between the first two is known (Brodkorb, 1934). Also, the celebrated "Carbonated Warbler" of Audubon has been thought to represent a hybrid Blackpoll $\times$ Cape May (for references see Cockrum, 1952:148). All are today restricted and highly adapted to northern coniferous forests, hence broadly sympatric. They are high rangers with thin, wiry songs dissimilar in form more than in quality. They nest variously from the ground (Blackpoll, occasionally) to very high (Cape May).

In terms of the model, it is conceivable that these species descended from a single eastern ancestor (could the Chestnut-sided Warbler, *Dendroica pensylvanica*, resemble this bird?) of the deciduous forest. Needed is only a history of adaptation, expansion, differentiation, re-expansion, etc., together with extinction of critical western differentiates and loss of eastern deciduous affiliations. We have seen evidence that all of these processes have occurred in various groups, and their occurrence in the right combination could account for the descent of the species here considered from a common ancestor.

Wilson's Warbler (*Wilsonia pusilla*) should be mentioned here also, because of its novel distribution. This distribution is unique in the family in embracing northern coniferous and western montane forests with no eastern vicariant species or well-marked subspecies. The northern race, *Wilsonia p. pusilla*, and the western montane *W. pusilla pileolata* are faintly marked and probably represent post-Wisconsin differentiation. The comparatively short migration route of the eastern race (no longer than that of the western one) and the distribution suggest that the northern range has been re-invaded from a western center of differentiation while the descendants of an eastern ancestral form are extinct. Neither congener (*Wilsonia citrina*, *W. canadensis*) seems close enough to qualify as such an ancestor.

Some General Considerations

It is further instructive to examine simultaneously the distributions of all the forms occurring in the areas considered, excluding a few kinds which are associated with grassy and shrubby environments, and whose distributions are unrelated to the thesis of this paper (e.g., the Yellow Warbler, *Dendroica petechia*; the Yellowthroat, *Geothlypis trichas*; the Yellow-breasted Chat, *Icteria virens*, which last may not be a warbler at all—Ficken and Ficken, 1962; and various southwestern, essentially Mexican forms such as the Red-faced Warbler, *Cardellina rubrifrons*).

Figure 8 shows graphically and Table 1 summarizes numerically the broad distributional relationships of the 46 wood warblers here considered, to the eastern deciduous, northern coniferous, and western montane forest regions. The figure illustrates a trend beginning with exclusive occupancy of eastern deciduous forest and ending with exclusive occupancy of western

TABLE 1
Summary of the Distributions of 46 Forest-adapted Wood Warblers

Distribution type	Regions occupied*	Number of species	Per cent of total	Number of species indigenous*		
				I	II	III
1	I	11	23.9	11		
2	I-II	14	30.4	14	14	1
3	I-II-III	1	2.2	1	1	
4	II	8	17.4		8	
5	III	10	21.7			10
6	III-II	2	4.4		2	2
Totals		46	100.0	26	25	13

*I = eastern deciduous forest; II = northern coniferous forest; III = western montane forest.

montane forest, with many intermediate situations and a few (those representing probable eastward re-expansions) situations suggesting a weak reciprocal trend.

It is of particular interest to note (1) that 11 deciduous forest species, potentially eligible for coniferous forest adaptation, have not yet exercised their franchises; (2) the gradual apparent loss of deciduous forest distribution and (presumably) adaptation in at least 15 species now attaining coniferous forest distributions and adaptations; and (3), particularly, the distributions of those birds whose occurrence across the northern coniferous forest eminently qualifies them for disjunction should another glaciation occur and thus begin a sequence of events like that of the model. At least 14 species certainly (those occurring all the way across the northern forest), and some 10 more possibly (those occurring more or less half way across), are now "waiting in the wings," so to speak, for the opening curtain of the next glaciation.

Two additional points are emphasized by Figure 8.

(1) No endemic genus occurs anywhere except exclusively or almost exclusively in the eastern deciduous forest which has no less than four (I am aware of course that these "genera" are no better than our taxonomy, but they do stand for special degrees of distinctness). This seems surely to indicate antiquity of the formation—and to a lesser extent of the region itself—as a center of distribution of the family.

(2) *Only one of the 12 endemic and/or probably autochthonous species of wood warblers of the western montane forests is without an obvious vicariant (e.g., modified descendant of a probable common ancestor) in the eastern deciduous and/or northern coniferous forest. (Only Wilson's Warbler, discussed above, provides an exception.) Conversely, not a single eastern form that has not acquired extensive coniferous forest adaptations possesses a vicariant or vicariants in the western montane forests, except the Yellow-throated Warbler. The peculiar circumstances concerning the last have been discussed above.*

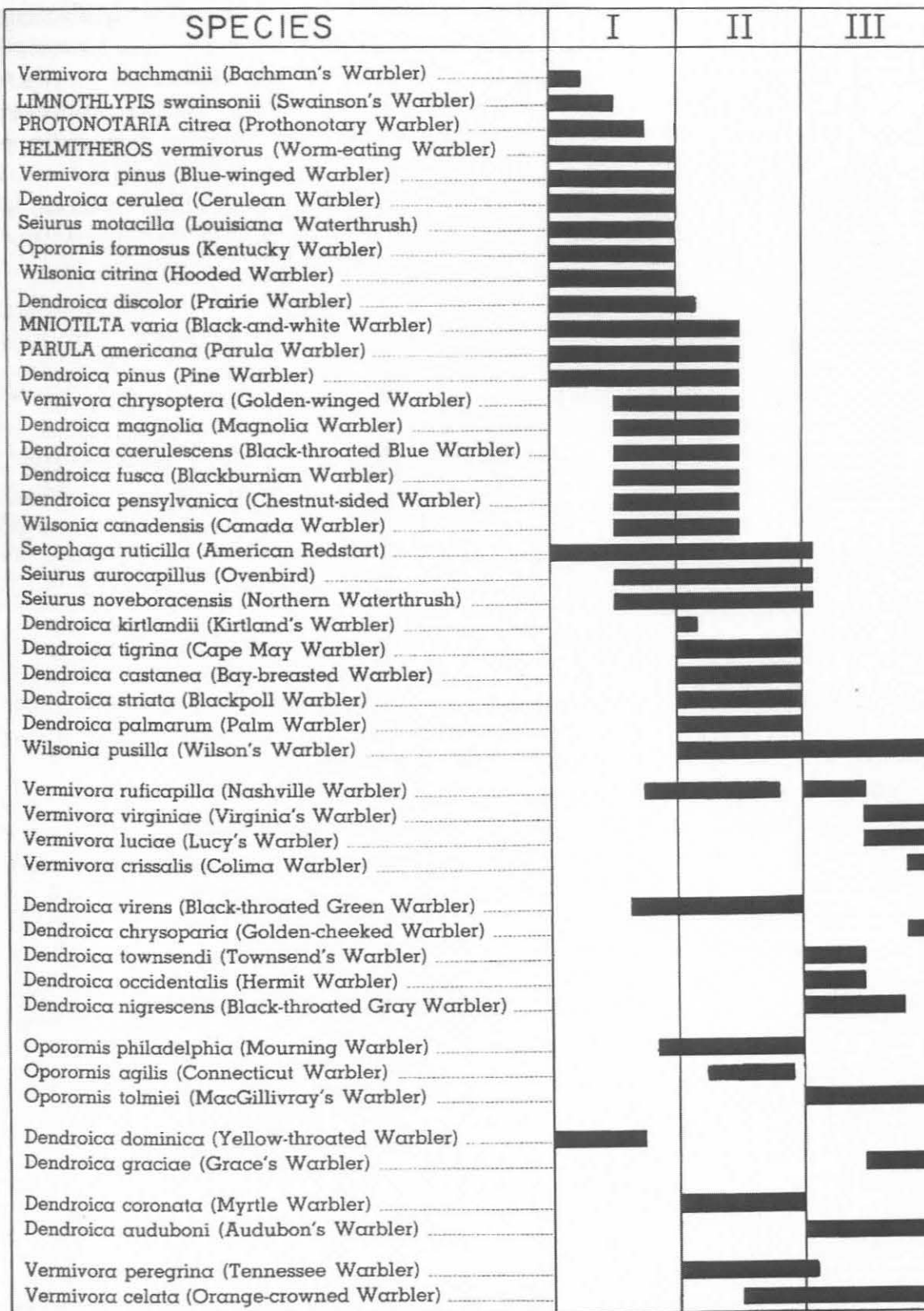


Figure 8. Generalized breeding distributions of 46 North American forest-adapted wood warblers in relation to the three great forest types of temperate and boreal North America (I, eastern deciduous forest; II, northern coniferous forest; III, western montane forests). Extension of a bar across a full column indicates occurrence through most or all of the region concerned; extension across part of a column indicates occurrence in part of the region, proximity to adjacent regions being indicated by the position of the bar. Genera set in capitals are endemic or nearly endemic to the eastern deciduous forest region. *Parula* is "endemic" only in the immediate context of the figure. The several species groups here discussed in detail are treated at the bottom and separated by spaces.

These are, then, additional indications of a broad, continental, historical pattern whose elements consist of (1) the eastern deciduous forest as an ancient center of wood warbler distribution and differentiation, (2) the northern coniferous forest as a recurrent corridor for expansion of species pioneering outward therefrom, (3) the western montane forests as a secondary center of distribution and (through glacial isolation) differentiation, and (4) the northern coniferous forest (more rarely) as a secondary center of differentiation for such western differentiates as again invade it only to be disjuncted once more by glacial advance.

Discussion

The model and some alternatives.—While this paper has been devoted particularly to suggesting the importance of the model and its northern route for western colonization, it would be a mistake, as already indicated, to explain all distributions in those terms. We have seen, in the case of the Yellow-throated-Grace's Warbler complex, species seemingly related historically not to northern forests but to woodlands derived from the old southern Madro-tertiary flora. Other wood warblers seem also to be related historically to this element.

The Parula Warbler (*Parula americana*), with both tropical (*P. pitiayumi*) and southwestern (*P. graysoni*) representatives, belongs here also, evidently. Other species that seem to belong with this group, although leaving no western representatives, are the pine and pine-oak inhabiting Pine, Prairie, and Kirtland's Warblers.

Numerous other members of the Madro-tertiary faunal element seem to have suffered disjunction as the once-widespread, southern woodland flora to which they were adapted was fractionated in the late Tertiary. For example, the Ivory-billed-Imperial Woodpecker group (*Campephilus principalis*-*C. imperialis*), with a West Indian representative of its own, is marvellously similar in distributional pattern to the Yellow-throated Warbler group, while less perfect parallels are offered by the scrub jays (Pitelka, 1951) and the pine-inhabiting pygmy nuthatches (*Sitta pygmaea*, *S. pusilla*) and certain ladder-backed woodpeckers (*Dendrocopos borealis*, *D. scalaris*-*D. nuttalli*).

In general, the more likely descendants of this Madro-tertiary fauna (for a list of some see Kendeigh, 1961:298) seem to have shown little tendency toward adaptation to northern coniferous or western montane coniferous forest, and the fauna has consequently had little success in northern colonization (Parula, Pine, and Kirtland's Warblers have done comparatively well in this direction).

It is probable, however, that not all species originally stemming from Madro-tertiary associated faunas have yet been identified. Some, perhaps early arrivals in the southeast, may early have been incorporated into the Arcto-tertiary forest community.

I have already indicated that Lucy's Warbler in the Nashville Warbler group and the Black-throated Gray Warbler in the Black-throated Green Warbler group may indeed be relicts resulting from the early (probably pre-Pleistocene) disjunction of a Madro-tertiary ancestor. The eastern differentiates, pro-*V. ruficapilla* and pro-*D. virens*, in such case, proceeding thereafter to follow the course of the model, would seem to be unique among descendants of the Madro-tertiary faunas in their exploitation of northern coniferous forest environments.

Some evidence in support of this line of thought may be that the Nashville

Warbler (like others of its group) is adapted to seral stages *in*, but not really *to*, northern coniferous or montane forests as such, as well as to edge situations in mixed deciduous-coniferous forest in the northeast. Likewise, the comparatively narrow niches (especially hemlock growth but including pine and pine-oak in some areas) occupied by the Black-throated Green Warbler in the eastern deciduous forest region may lend some support to this theory, as does the peculiar cedar brake, oak-scrub habitat of the very similar Golden-cheeked Warbler.

We must, further, not suppose that even both of the above-mentioned processes (Arcto-tertiary origins, northern route; Madro-tertiary origins, disjunction of a southern ancestor), singly or in combination, account for all northern, late Cenozoic wood warbler differentiation. Various cases seem to fall wholly outside the framework of the present discussion. For example, Short (1963) has provided a tempting hypothesis for Pleistocene isolation and differentiation, in the *east alone*, of the Blue-winged and Golden-winged Warblers, and similar processes, even if obscure, may have accounted for additional speciation.

(It is, finally, not inconceivable that one or two species have made the adaptation *directly* from western Madro-tertiary woodland affiliations to western montane coniferous forest environments—the strange little Red-faced Warbler of southwestern mountains is a likely candidate—but indications are that this must have happened very rarely indeed and with limited success.)

Ecological considerations.—Emphasis thus far has been zoogeographical, that is, upon the trends and distributions of species. It should not be overlooked, however, that the zoogeographical trends of expansion and adaptation of species from deciduous to coniferous forest, hence northward and westward, is reflected ecologically by a marked gradient in population densities. As individuals, wood warblers, among the most numerous birds in typical eastern forests (including the northern coniferous climax in its eastern portion), are comparatively scarce in western coniferous forests, and progressively so with increase in elevation. There is thus a clear gradient in their population densities across the northern coniferous forests. This is inversely correlated with a trend in the densities of the cold-adapted Eurasian autochthones such as the tits, nuthatches, cardueline finches, and kinglets (Snyder, 1950), which historically may have been competitors for space in these coniferous forests.

In this connection, it may be supposed also, as more and more wood warblers have made the postulated adaptations and ventured with varying success across the northern route, that the process would become increasingly difficult when new pioneers encountered more and more well-entrenched predecessors. Thus we may well marvel at the capacity of the group at subtle niche diversification permitting extensive sympatry of nearly related forms, as shown specifically by MacArthur (1958) and demonstrated generally by the presence in some Appalachian regions of as many as 17 breeding species in a few square miles of comparable elevation (pers. obs.).

Equally, it seems that the tasks of western differentiates recrossing the northern route eastward would be especially difficult for the same reasons, since more and more potential competitors would be encountered in progressing toward the east. This may account in part for the apparent rarity of the event. Also, it should be recalled that (a) the supply of western species is much smaller; (b) they tend to be isolated by elevation during interglacial optima; and (c) their adaptations to the comparatively specialized montane

environments may have unfitted them for recolonization of northern coniferous forest. It is perhaps significant that those forms which seem most likely to have accomplished eastward re-invasion (Orange-crowned, Wilson's, and Mourning Warblers) are adapted to seral stages, which are well known (Pitelka, 1941:131; Odum, 1945:198) to be more uniform in type than are climaxes, and which likewise are less liable to interglacial, montane isolation.

The origin of the Parulidae.—A few remarks on the history of the family may be ventured. The origin of the family in the North American tropics was postulated by Lönnberg (1927) and reaffirmed by Mayr (1946:21-22). Characteristics of the group here brought into focus support this hypothesis and, additionally, suggest a little about the timing of this origin.

If the Parulidae had been in existence and very early adapted to the temperate or (especially) boreal elements of the Arcto-tertiary forests, it would be remarkable not to find some of them in Asia, and many more than we do in western North America. We must, therefore, suppose that the group, arising from Neotropical-tertiary and Madro-tertiary forests, began its adaptations to the temperate Arcto-tertiary forests after these forests had been fractionated by climatic deterioration and mountain-building. This process of fractionation began in the Miocene and gained impetus through the Pliocene.

At the same time, however, a comparatively early appearance (e.g., probably by the early Pliocene) of the group, in considerable force, in the temperate Arcto-tertiary forests is still indicated. Otherwise it is difficult to account for the abundance of species and genera restricted today and exclusively adapted to the remnantal eastern deciduous forest; invasion of this forest from more tropical formations would have become increasingly difficult for tropical forms and, by late Pliocene time, highly improbable as the deciduous forest became isolated by broad grasslands and other xerophytic formations extending to the Gulf of Mexico.

All of this seems to point to an early mid-Tertiary origin of the group (perhaps in the late Oligocene or early Miocene) in Neotropical-tertiary and perhaps Madro-tertiary forests of southern North America, with the more progressive and rapidly evolving members invading the shrinking Arcto-tertiary forests in the later part of the mid-Tertiary (late Miocene, early Pliocene), where they were to await the advent of the Pleistocene before embarking upon the radiation postulated in this paper.

Here it is tempting to theorize, invoking "Matthew's hypothesis" (Matthew, 1939: many pp., but see especially 140-144), that it is just in these Arcto-tertiary forests, near the end of the Tertiary, that we should look for those progressive and adaptable members of the group most capable of evolving in the face of changing conditions and of capitalizing upon the evolutionary opportunities stressed in this paper. The less plastic and more primitive members of the group would have retreated deep to the south where, perhaps, we find them today in the form of such genera as *Basileuterus*, *Euthlypis*, *Granatellus*, *Myioborus*, etc.

Miscellaneous observations.—Various elements of the evidence here considered provide indications of possible significance to other aspects of Pleistocene biogeography.

For instance, while I readily grant that circularity of reasoning is being skirted, the pattern of western differentiates here indicated (in which several degrees of distinctness are discernible, suggesting varying antiquities of disjunction and hence repeated use of the northern route of the model) seems

to argue that the northern coniferous forest as we know it today, or nearly so, may in fact be considerably older than the Wisconsin glacial retreat. This is a logical enough assumption and one made by many authors but, because of the tendency of each glacier to eradicate the underlying tills of its predecessors, there is still little concrete evidence for it (Braun, 1950:511).

Likewise, the survival of a comparatively unmodified array of Arcto-tertiary temperate elements over much of the southeastern glacial refugium throughout the Pleistocene is strongly suggested by the number of surviving parulids fully adapted and solely or largely restricted to the eastern deciduous forest of today. While a whole essay could and should be devoted to this subject, it is here possible only to say that it is extremely difficult to imagine this large, diverse, and closely-adapted fauna gaining its present distribution and degree of adaptation since the Wisconsin, much less regaining these three or four times. Thus Deevey's view (1949:1371-1375) *contra* Braun (1947; 1950:512-520; 1955) that the Arcto-tertiary temperate (= mixed mesophytic forest of today *sensu* Braun, 1950:39-121) was radically altered throughout, if not essentially obliterated as an integral community, by invasion of northern floral elements during glacial maxima seems less plausible than the slightly more moderate view of Martin (1958:383, Figure 2), and than the still more moderate compromise indicated by Kendeigh (1961:285, Figure 21-2).

Antiquity of speciation.—Finally, all of the evidence presented suggests that Wetmore's statement (1959:21-22) that most modern bird species were probably already in existence at the beginning of the Pleistocene needs modification, at least with reference to the higher passerines, and especially those of northern distribution. In the present case the suggestions are that at least 10 (22 per cent) and possibly as many as 17 (37 per cent) of the 46 species of continental wood warblers here considered have achieved their specific distinctness directly as a result of Pleistocene events.

This number might well be greater were it not for the probability of many extinctions. We see that today four species of wood warblers considered are relicts liable to extinction with the slightest unfavorable turn of events (Kirtland's, Golden-cheeked, and Colima Warblers, and the previously-unmentioned Bachman's Warbler, *Vermivora bachmanii*). Allowing four extinctions per glacial cycle, it is possible that there are today no less than 12 ghosts in the parulid fauna of North America; how much the distributions and characters of these spirits might tell us, if they were living birds!

In Summary

The distributions and relationships of 46 continental and 2 insular species of forest-adapted wood warblers are considered in relation to the Tertiary and Pleistocene history of North America, and the implications to Pleistocene biogeography in general are briefly discussed. The following hypothesis is developed and defended.

At the close of the Pliocene there were two elements in that part of the family Parulidae occurring in North America: A large, more northern element adapted to the remnantal temperate (deciduous) Arcto-tertiary forest in eastern North America and a smaller, more southern element adapted to recently disjuncted western and eastern sclerophyll woodlands derived from the Madro-tertiary (relatively xerophytic deciduous) flora. Some species, notably Grace's Warbler and possibly the Black-throated Gray and Lucy's Warblers owe their differentiation from eastern stocks to the latter disjunction.

With the advent of Pleistocene glaciation, boreal (northern coniferous)

elements of the Arcto-tertiary forest were forced deep into the southeast, invading a compacted temperate Arcto-tertiary forest (henceforth equated with today's eastern deciduous forest) and permitting development of adaptations to coniferous forest or its seral stages by some of the wood warblers living there.

Upon glacial recessions, broad, transcontinental bands of boreal Arcto-tertiary forest (henceforth equated with northern coniferous forest) were established in the wake of the retreating ice (western montane coniferous forests similarly replaced the mountain glaciers) and these were occupied by the newly-adapted wood warblers. These birds thereby achieved immense, continent-spanning ranges (comparable to many seen today) that permitted disjunction of the stocks into separate eastern and western refugia upon subsequent glacial advance. Differentiation occurred in these refugia, and some western differentiates were further isolated, during the warm interglacial periods, in western montane coniferous forests as these withdrew up the mountain slopes into separate "islands." Other, though fewer, western differentiates re-invaded the northern coniferous forest and again achieved wide distributions, only to be disjuncted once more.

Repetition of this process through four glacial cycles resulted in the differentiation of all or nearly all of the endemic and/or autochthonous western species of wood warblers (aside from Grace's Warbler) of which 12 survive (others have probably become extinct). These are: the Townsend's, Hermit, and possibly Black-throated Gray Warblers of the Black-throated Green Warbler group; the western race of the Nashville Warbler, and the Virginia's, Colima, and possibly Lucy's Warblers of the Nashville Warbler group; the MacGillivray's Warbler of the Connecticut Warbler group; Audubon's Warbler of the Myrtle Warbler group; the Orange-crowned Warbler of the Tennessee Warbler group; and the Wilson's Warbler. The Golden-cheeked Warbler of Texas was separated and differentiated from the ancestors of the Black-throated Green Warbler recently, probably since the Wisconsin (most recent) glaciation.

Possibly the Blackpoll, Bay-breasted, and Cape May Warblers are products of similar processes, but descendants of very probable ancestors adapted to eastern deciduous forest are lacking and possibly extinct.

The eastern Mourning Warbler seems likely to be descended from a western differentiate (e.g., the fore-runner of MacGillivray's Warbler) re-invading eastward, and the Myrtle Warbler may be also. The Orange-crowned and Wilson's Warblers are today evidently re-invading eastward from western centers of differentiation, but the latter leaves no eastern vicariant, being, in this respect, unique among western wood warblers.

The eastern forms descending directly from the eastern ancestral stocks responsible for the several westward invasions (Black-throated Green, Nashville, Connecticut, possibly Myrtle, and Tennessee Warblers) have tended progressively to lose their original deciduous forest adaptations and distributions. This is true also, to usually lesser but varying degrees, of at least 15 species currently invading the northern coniferous forest and liable themselves to disjunction and differentiation in case of subsequent glaciation.

The differentiation of between 10 (22 per cent) and 17 (37 per cent) out of 46 species indicates a high rate of Pleistocene speciation in the northern Parulidae and suggests that higher passerine species formation may have been more extensive in the Pleistocene than has heretofore been thought.

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